

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXVI, No. 15, pp. 391-500; 60 figs.

April 18, 1969

OSTEOLOGY AND RELATIONSHIPS OF
CHARACOID FISHES, PARTICULARLY THE
GENERA *HEPSETUS*, *SALMINUS*, *HOPLIAS*,
CTENOLUCIUS, AND *ACESTRORHYNCHUS*

By

Tyson Roberts

Division of Systematic Biology, Stanford University, California 94305

TABLE OF CONTENTS

| | Pages |
|--|-------|
| LIST OF FIGURES | 393 |
| ACKNOWLEDGMENTS | 395 |
| INTRODUCTION | 396 |
| METHODS AND MATERIALS | 401 |
| CRANIUM | 405 |
| Ethmoid region | 405 |
| Rhinosphenoid | 406 |
| Parasphenoid | 406 |
| Cranial sculpturing | 407 |
| Cranial fontanel | 407 |
| Epiphyseal bar | 407 |
| Lateral margin of the cranial roof | 408 |
| Sphenotic bone and dilator groove | 408 |
| Parietal bones | 410 |
| Supraoccipital bone | 411 |
| Note on squamation on the head | 411 |
| Slope of the occiput | 412 |
| Posttemporal fossae | 412 |
| Subtemporal fossa | 413 |
| Intercalar bone | 414 |

TABLE OF CONTENTS (*Cont'd.*)

| | Pages |
|--|-------|
| JAWS | 414 |
| General features | 414 |
| Symphyseal hinge joint | 416 |
| SUSPENSORIUM AND PALATAL BONES | 417 |
| Ectopterygoid teeth | 418 |
| Symplectic bone | 418 |
| FACIAL BONES | 419 |
| Nasal bone | 419 |
| Circumorbital bones | 419 |
| Opercular bones | 421 |
| Subopercle | 421 |
| HYOID ARCH | 421 |
| Basihyal | 421 |
| Branchiostegal rays | 422 |
| GILL ARCHES | 422 |
| General features | 422 |
| Gill rakers | 423 |
| Pharyngeal teeth | 424 |
| WEBERIAN APPARATUS | 424 |
| PECTORAL FIN | 426 |
| PELVIC FIN | 427 |
| CAUDAL FIN | 427 |
| Hypurals | 427 |
| Uroneurals | 428 |
| Epurals | 428 |
| Procurent caudal rays and associated structures | 428 |
| CHARACTERISTICS OF THE PRIMITIVE AFRICAN FAMILY HEPSETIDAE | 429 |
| CHARACTERISTICS OF THE AMERICAN FAMILY CTENOLUCIIDAE | 431 |
| COMMENTS | 432 |
| RELATIONSHIP OF HEPSETIDAE AND CTENOLUCIIDAE | 433 |
| COMPARISON OF BOULENGERELLA AND CTENOLUCIIDAE | 434 |
| RELATIONSHIPS OF SALMINUS | 435 |
| CATABASIS | 437 |
| REMARKS ON BRYCON ACUTUS BÖHLKE | 438 |
| SPACING OF THE JAW-TEETH IN CHARACOIDS | 439 |
| RELATIONSHIPS OF ACESTRORHYNCHUS | 440 |
| REMARKS ON AFRICAN CHARACIDAE | 441 |
| CONCLUSIONS | 442 |
| FIGURES | 444 |
| LITERATURE CITED | 497 |

FIGURES

| | Pages |
|---|-------|
| 1 <i>Hepsetus odoe</i> , skull in lateral view | 444 |
| 2 <i>Ctenolucius hujeta</i> , skull in lateral view | 445 |
| 3 <i>Hoplias</i> species, skull in lateral view | 446 |
| 4 <i>Salminus brasiliensis</i> , skull in lateral view | 447 |
| 5 <i>Acestrorhynchus</i> species, skull in lateral view | 448 |
| 6 <i>Hepsetus odoe</i> , skull in dorsal view | 449 |
| 7 <i>Ctenolucius hujeta</i> , skull in dorsal view | 450 |
| 8 <i>Hoplias</i> species, skull in dorsal view | 451 |
| 9 <i>Salminus brasiliensis</i> , skull in dorsal view | 452 |
| 10 <i>Acestrorhynchus</i> species, skull in dorsal view | 453 |
| 11 <i>Hepsetus odoe</i> , cranium in lateral view | 454 |
| 12 <i>Ctenolucius hujeta</i> , cranium in lateral view | 455 |
| 13 <i>Hoplias</i> species, cranium in lateral view | 456 |
| 14 <i>Salminus brasiliensis</i> , cranium in lateral view | 457 |
| 15 <i>Acestrorhynchus</i> species, cranium in lateral view | 458 |
| 16 <i>Hepsetus odoe</i> , cranium in ventral view | 459 |
| 17 <i>Ctenolucius hujeta</i> , cranium in ventral view | 460 |
| 18 <i>Hoplias</i> species, cranium in ventral view | 461 |
| 19 <i>Salminus brasiliensis</i> , cranium in ventral view | 462 |
| 20 <i>Acestrorhynchus</i> species, cranium in ventral view | 463 |
| 21 <i>Hepsetus odoe</i> , occipital region of skull | 464 |
| 22 <i>Ctenolucius hujeta</i> , occipital region of skull | 464 |
| 23 <i>Hoplias</i> species, occipital region of skull | 464 |
| 24 <i>Salminus brasiliensis</i> , occipital region of skull | 465 |
| 25 <i>Acestrorhynchus</i> species, occipital region of skull | 465 |
| 26 <i>Hepsetus odoe</i> , jaws and deeper facial bones | 466 |
| 27 <i>Hepsetus odoe</i> , internal view of lower jaw | 466 |
| 28 <i>Ctenolucius hujeta</i> , jaws and deeper facial bones | 467 |
| 29 <i>Hoplias</i> species, jaws and deeper facial bones | 468 |
| 30 <i>Hoplias</i> species, internal view of lower jaw | 468 |
| 31 <i>Salminus brasiliensis</i> , jaws and deeper facial bones | 469 |
| 32 <i>Acestrorhynchus</i> species, jaws and deeper facial bones | 470 |
| 33 <i>Hepsetus odoe</i> , hyobranchial apparatus | 471 |
| 34 <i>Ctenolucius hujeta</i> , hyobranchial apparatus | 472 |
| 35 <i>Hoplias</i> species, hyobranchial apparatus | 473 |
| 36 <i>Salminus brasiliensis</i> , hyobranchial apparatus | 474 |
| 37 <i>Acestrorhynchus</i> species, hyobranchial apparatus | 475 |
| 38 <i>Hepsetus odoe</i> , Weberian apparatus in lateral view | 476 |
| 39 <i>Hepsetus odoe</i> , Weberian apparatus in ventral view | 477 |
| 40 <i>Ctenolucius hujeta</i> , Weberian apparatus in lateral view | 478 |
| 41 <i>Ctenolucius hujeta</i> , Weberian apparatus in ventral view | 479 |

| FIGURES | Pages |
|---|-------|
| 42 <i>Hoplias</i> species, Weberian apparatus in lateral view | 480 |
| 43 <i>Hoplias</i> species, Weberian apparatus in ventral view | 481 |
| 44 <i>Salminus brasiliensis</i> , Weberian apparatus in lateral view | 482 |
| 45 <i>Salminus brasiliensis</i> , Weberian apparatus in ventral view | 483 |
| 46 <i>Acestrorhynchus</i> species, Weberian apparatus in lateral view | 484 |
| 47 <i>Acestrorhynchus</i> species, Weberian apparatus in ventral view | 485 |
| 48 <i>Hepsetus odoe</i> , pectoral girdle | 486 |
| 49 <i>Hepsetus odoe</i> , pectoral girdle of 42 mm. specimen | 487 |
| 50 <i>Ctenolucius hujeta</i> , pectoral girdle | 488 |
| 51 <i>Hoplias</i> species, pectoral girdle | 489 |
| 52 <i>Acestrorhynchus</i> species, pectoral girdle | 490 |
| 53 <i>Hepsetus odoe</i> , pelvic girdle | 491 |
| 54 <i>Ctenolucius hujeta</i> , pelvic girdle | 491 |
| 55 <i>Hoplias</i> species, pelvic girdle | 491 |
| 56 <i>Hepsetus odoe</i> , caudal skeleton | 492 |
| 57 <i>Ctenolucius hujeta</i> , caudal skeleton | 493 |
| 58 <i>Hoplias</i> species, caudal skeleton | 494 |
| 59 <i>Salminus brasiliensis</i> , caudal skeleton | 495 |
| 60 <i>Hydrocynus</i> species, caudal skeleton of a 20 mm. specimen | 496 |

ACKNOWLEDGMENTS

This work is part of a doctoral dissertation done at Stanford University under the direction of Professor George S. Myers. Professor Myers' extensive personal knowledge of characoids has been of considerable assistance. His comments frequently either led me to find out something or directed me away from less fruitful inquiries. For his help and encouragement I am deeply grateful. I must also express gratitude for being allowed to make free use of the collections of fishes under his care in the Division of Systematic Biology.

I have benefited from discussions or helpful criticism of my work and encouragement from Dr. A. Kent Christensen, Stanford Department of Anatomy, and Dr. Warren C. Freihofner, Division of Systematic Biology, Stanford, both members of my dissertation committee; and from Dr. Stanley H. Weitzman, Division of Fishes, U. S. National Museum. Dr. Jacques Géry first encouraged me to devote my thesis to characoids and interested me in their teeth.

For providing working space and facilities in his laboratory and for his encouragement, I wish to thank Stewart Springer of the U. S. Bureau of Commercial Fisheries, formerly at Stanford. Mrs. Mary Wagoner, his staff illustrator, generously instructed me on how to prepare illustrations and helped out in other ways.

While studying this complex and beautiful group of fishes, I have come to appreciate the ichthyologists of the past who have studied them—Cuvier and Valenciennes, Müller and Troschel, Agassiz, Kner, Steindachner, Sagemehl, Boulenger, Regan, Eigenmann. These men must have felt the fascination and pleasure of discovery still awaiting anyone who will delve into the study of characoids.

INTRODUCTION

Biogeographic evidence has played an historically important role in the continuing debate over Continental Drift. Although the main arguments for or against Drift must come from geologic considerations, the possibility that plant and animal distributions reflect continental geography prior to episodes of Continental Drift is inherently fascinating. The distribution of characoids, a well-defined group of primary freshwater fishes which are extremely numerous in Africa and South America, represents perhaps the strongest zoogeographic evidence corroborating the hypothesis that these two continents were once a single land mass.

Except for their relatively recent invasion of Central America, characoid fishes have probably always been confined to Africa and South America, where they are old and dominant elements of the ichthyofauna (Myers, 1966). The tremendous diversity of characoids—about 30 genera in Africa and over 250 in South America—is indicative of great age. It should also be noted that in South America the characoids have given rise to the gymnotoids, a group accorded subordinal status by Greenwood and others (1966). I believe that characoids existed before Africa and South America were separated by the last episode of Continental Drift, although no Mesozoic characoid fossils have been found. That the South American and African characoids have long been in isolation from each other is evident, for of the 16 characoid families recognized by Greenwood and his coauthors, only one of them (the Characidae) is found in both continents. The African and South American members of this family appear to represent different subfamilies. The present work is an effort to help unravel the exceedingly complex phylogeny of characoids.

I have recently published a study of tooth formation and replacement in characoid fishes (Roberts, 1967a). These topics had previously received relatively little attention, although to anyone familiar with characoids it is evident that trophic specialization played a major role in the evolution of the higher categories of this group. Even among vertebrates as a whole, the diversity and range of complexity of characoid teeth is truly astounding. The modes of tooth formation and replacement characteristic of characoids apparently arose early in their history and provided the main morphological basis for extensive adaptive radiations. Valuable clues to the phylogeny of characoids often can be found by studying the morphology of their teeth at various ontogenetic stages. Whereas the majority of living forms have complex multicuspid teeth, it would appear that characoids primitively had conical teeth.

In the present work descriptions and figures are given of the osteology of five genera of characoids which have conical teeth, and an attempt is made to understand some of the general evolutionary trends that have affected characoid

osteology. There has been a great need for accurate morphological information about characoids (Weitzman, 1962, pp. 7, 8). Time did not permit thorough osteological study of as many characoids as interest alone would have dictated. Detailed study was concentrated on the genera *Hepsetus*, *Ctenolucius*, *Acestrorhynchus*, *Salminus*, and *Hoplias* because it was felt they would provide more useful information for understanding broad problems of characoid phylogeny than would any other genera.

Hepsetus is phylogenetically the most isolated of all African characoids, and its dentition appears to be primitive. (Hubbs, 1939, pointed out that *Hepsetus* Swainson, 1838, antedated *Sarcodaces* Günther, 1864, and indubitably pertains to the same genus). *Ctenolucius*, except for its more specialized but still close relative *Boulengerella*, is anatomically among the most isolated of American characoids, and in certain respects it resembles *Hepsetus*. It has not been clear, however, whether the resemblances between *Hepsetus* and *Ctenolucius* are due to relationship or convergent evolution; the considerable osteological differences between them have not hitherto been elucidated. Because of its pike-like habitus, *Acestrorhynchus* superficially resembles *Hepsetus* and *Ctenolucius*, but it is apparently related to such specialized characids as *Charax*, *Rocbooides*, and certain others with rapacious conical dentition. The relationships of *Acestrorhynchus* and this important group of predaceous characoids with each other and with other characoids has been problematical. *Salminus* belongs to the family Characidae and has what appears to be primitively conical dentition. Its relationships to other members of the Characidae have not been clear. *Hoplias* was chosen as a typical representative of the family Erythrinidae, a small, phylogenetically isolated American family which has been considered primitive by various authors. In numerous instances, information about additional characoids, other teleostean groups, or *Amia* has been given to help illustrate osteological trends.

The differences exhibited by a few bony structures do not appear to be particularly helpful in phylogenetic analyses of characoids, at least not until data concerning them can be gathered from a greater number of genera, and these structures have been left out of this study. These are the otoliths, dorsal and anal fin supports, vertebrae, and intermuscular bones. The lapillus, sagitta, and asteriscus of *Hoplias* (Adams, 1940, fig. 1) are very similar to those of the characid *Brycon mecki* (Weitzman, 1962, fig. 7).

In general I have had little to say about the ontogeny of characoid skeletal parts; this is a subject which merits study. Bertmar (1959) published a detailed description of the development of the chondrocranium in *Hepsetus*, and on this basis compared the characoid chondrocranium with that of various other fishes. Unfortunately, information about the chondrocrania of characoids other than *Hepsetus* is still too meager to be used for phylogenetic analysis.

The discussion deals more specifically with the relationships of *Hepsetus*, *Ctenolucius*, *Salminus*, and *Acestrorhynchus*. Evolutionary trends and relationships of other characoids are also considered in the light of their dentition and osteology.

As in most groups of organisms with a complex phylogenetic history, characoids present many characters with an irregular or mosaic distribution. That is, similar characters have arisen independently in various groups of characoids. This is particularly true of what may be termed "reduction characters" and "loss characters." One such character, the incomplete lateral line (involving failure of scales overlying the lateral line canal to form pores) has recently been discussed in detail (Roberts, 1967b). Characoid osteology offers numerous examples of loss and reduction characters which have occurred repeatedly: loss of branchiostegal rays and epurals; fusion of circumorbital bones or their reduction to simple bony tubes enclosing a portion of the cephalic lateral line; loss of the antorbital or its fusion with the first circumorbital to form a single bone; reduction of multicuspid teeth to conical teeth; and loss of teeth or of entire tooth rows. The presence of but a single postcleithrum in the pectoral girdle of Hepsetidae and Ctenoluciidae may be due to independent loss. Much of the faultiness in Eigenmann's concepts of characoid genera and higher categories was due to reliance on single characters, often loss or reduction characters, which have tended to arise independently. It is evident from his later papers that Eigenmann became increasingly cognizant of the difficulties involved in the use of such characters in taxonomy.

It should be understood that the subjection of a character to loss or reduction in some lines does not preclude its usefulness in understanding relationships, even major relationships. In most African Characidae and in the American characid subfamilies Bryconinae and Tetragonopterinae, and in the genera *Metynnias*, *Myloplus*, *Myleus*, *Colossoma*, and *Piaractus* of the subfamily Serrasalminae, the mandibles usually have a pair of more or less large conical teeth near the symphysis and internal to the external tooth row. The presence of these teeth supports the presumed relationship of African and American characoids that have been assigned to the family Characidae, and they are probably a primitive feature. They have been lost more than once in both American and African characids. They are absent in some species that I would definitely assign to the genus *Brycon*, and may have been lost more than once in that genus.

In no way can all characters with a mosaic distribution in characoids be ascribed to loss or reduction. Elongation of the jaws and snout, sometimes correlated with changes in dentition, has recurred repeatedly. In the extreme elongation of the jaws in *Ctenolucius* and *Belonophago*, the similarities are obviously parallelisms. *Belonophago* is a specialized relative of the relatively short-snouted

ichthyorid *Phago*, and the Ichthyoridae (entirely African) are not directly related to the American Ctenoluciidae. In the characids *Brycon acutus*, *Bramocharax*, *Catabasis*, and *Accestrorhamphus*, however, it seems likely that moderate elongation of the jaws and snout and lateral compression of the head and body have occurred independently. At first glance all of these fishes are strikingly similar. Their exact relationships to each other and to other American Characidae are far from clear. Conversely, foreshortening of the jaws (sometimes correlated with the development of relatively massive or even molariform multicuspid teeth) probably also has occurred independently in Characidae. Increases in the number of rows of functional teeth and evolution of teeth with numerous cusps and fan-shaped bases have also occurred several times in characoids.

The Greenwood and others (1966) familial classification of characoids has been followed throughout this work. This classification is apparently a good one and is in accordance with present knowledge of the characoids. On the whole the morphological differences between the various groups of characoids recognized as separate families in this classification are of sufficient magnitude as to justify full familial rank. Other groups of teleosts, particularly among the Percomorphi, are recognized as families on the basis of morphological distinctions which I would consider less significant than those distinguishing the families of characoids.

Greenwood and others did not define the families they recognized. A definition of the family Characidae was given by Weitzman (1962), and the families Lebiasinidae and Erythrinidae were defined by Weitzman (1964). (In these papers the families were assigned subfamilial rank.) Definitions of the Hephsetidae and Ctenoluciidae, based largely on osteology, are given in the present work. It is probable that some characoid genera will have to be transferred from one family to another, and there is a faint possibility that some of the families (the Characidae, for example) should be split still further. A great amount of work remains to be done before the American subfamilies of Characidae can be understood, a subject which is touched on in this paper only with regard to *Salminus*, *Brycon*, and *Accestrorhynchus* and its allies. I have not attempted to work out subfamilies of American Characidae. Further shuffling of genera and erection of subfamilies within the American Characidae will serve no useful purpose until such actions are supported by morphological studies. Reasonably complete osteological studies of certain key genera would be very useful.

Greenwood and others did not discuss the phylogeny or interrelationships of the fish families recognized by them. Weitzman, who was primarily responsible for the section dealing with characoids, has stated (personal communication) that the order in which the families were listed (pp. 395–396) was in part intended to indicate relationships. Thus Hephsetidae and Ctenoluciidae, which he

regarded as probably related, were listed together. Greenwood and others did not indicate the principal genera or even the subfamilies which they would assign to the various families. This will not be a source of confusion to workers familiar with characoids, for all of the families excepting Characidae represent relatively small, discrete groups of fishes which are readily recognizable. The reader is referred to Weitzman (1960a, p. 218, footnote 1) for a list of the subfamilies tentatively assigned to the Characidae.

Weitzman (1962, pp. 8, 9) summarized the literature on characoid osteology. For various reasons cited by him—inaccuracy, superficial treatment, or ill-advised choice of subjects for investigation—most of this literature provides little useful information for considerations of characoid phylogeny. By far the most useful papers on characoid osteology are those by Sagemehl (1885), Regan (1911), and Weitzman (1954, 1962, 1964). Papers dealing with characoid osteology that have appeared subsequent to Weitzman (1962) are Géry (1963a, 1963b, 1963c), Weitzman (1964), Alexander (1965), and Roberts (1966).

At the beginning of my research on characoids I believed that information for analysis of their phylogeny could be more readily gained from comparative osteological studies than by any other approach. Judging from the resurgence of studies of this kind, it is evident that similar feelings are shared by ichthyologists concerned with other groups of bony fishes. There still are major groups of teleosts for which osteological information is scanty, and many genera of presumably phylogenetic importance for which it is wanting entirely.

The usual approach in studies on fish osteology, and one that I have generally followed, is to treat the skeleton as a relatively static system without regard to the considerable ontogenetic changes that sometimes occur in it. A notable exception to this tendency is the recent paper by Berry (1964) on the development of teleostean upper jaw bones. I have studied ontogenetic skeletal changes in a few instances with rewarding results. In studies on characoid dentition, of course, ontogenetic changes are of primary importance. I suspect that developmental information about skeletal features will be useful in working out characoid phylogeny, but that the most useful information of this kind will come from the teeth, which reflect in their ontogeny much concerning characoid relationships.

The work on osteology presented herein is incomplete in that the relationships of the bones to cartilage, nerves, muscles, ligaments, and other soft structures have not been taken consistently into consideration. Ideally bones should not be studied as isolated structures, although this is the course generally followed by students of fish osteology. Much of teleostean phylogeny has involved considerable changes in bony structures, and these changes often cannot be properly understood without reference to other structures. One is also faced with the manifold problems of functional anatomy. The few observations we

have on the functional anatomy of characoids are mostly to be found in a recent paper by Alexander (1965). Further work of this kind is needed, preferably at the experimental level with living fishes. The technical difficulties in experimenting with live fishes present challenges worthy of ingenious experimenters. Much, of course, can be done to understand functional anatomy of fishes through purely anatomical study when live specimens are unavailable, as evidenced by the study of the feeding mechanism of the deep-sea fish *Chauliodus sloani* by Tchernavin (1953). Such studies add greatly to our understanding of the biology of fishes, and they may also be extremely illuminating for the student of phylogeny. Foremost among the problems of functional anatomy to be tackled in characoids are those involving feeding, since trophic specialization has played a major role in their adaptive radiation. These studies must be correlated with observations on the feeding behavior, foraging locations and types of food taken. For the majority of characoids such information is scanty or non-existent; too often information concerning food habits is untrustworthy or anecdotal.

METHODS AND MATERIALS

As indicated in the introduction, it has not been my intention to give complete osteological accounts of *Salminus*, *Hepsetus*, *Hoplias*, *Ctenolucius*, and *Acetrorhynchus*. For a relatively complete account of the osteology of a generalized characoid fish, the reader is referred to Weitzman (1962). Studies on the nerves and blood vessels were not carried out to complement the present study of the bones, and until more is known about these structures it seems unwise to identify cranial foramina in characoids by tenuously extrapolating from what is known about other fishes. The decision to omit the otoliths, vertebrae exclusive of the Weberian apparatus, intermuscular bones, and endoskeletal supports of the dorsal and anal fins was not entirely arbitrary. After preliminary studies of these structures it seemed that they offered relatively little insight into the major problems of phylogeny under consideration. This should not be construed to mean that studies of these structures will fail to provide fresh insights into other groups of characoids. The otoliths and other structures may possess instructive features which have been overlooked, so that they should not invariably be excluded from consideration in future studies of characoids. The exceptionally well developed zygapophyses on the abdominal vertebrae in members of the family Cynodontidae are worthy of further study.

In the present study major attention has been focused on osteological features which seem to be of greatest phylogenetic and taxonomic significance. Thus there are extensive descriptions of the lateral margin of the cranial roof, of the dilator groove, of the circumorbital bones and their articulation to the skull, and of the relationship of the maxillary bone to the anterior infraorbital bones. Certain modifications of these structures are evidently phylogenetically and func-

tionally interrelated; I feel that understanding the nature and interrelations of the changes that have occurred in various groups of characoids will provide significant phylogenetic insights.

The osteological terminology used in this paper, with two exceptions, is identical with that of Weitzman (1962). The exceptions are the use of "vomer" and "intercalar" in place of "prevomer" and "opisthotic." These changes have been recommended by Weitzman (personal communication).

Specimens of *Hepsetus*, *Ctenolucius*, *Acestrorhynchus*, *Salminus*, and *Hoplias* were prepared for osteological study by macerating and staining them in alizarin-potassium hydroxide solution and then clearing them in glycerin. In certain instances it was found useful after such treatment to dissect the non-bony tissue from a specimen and then return it to the alizarin-potassium hydroxide solution to pick up more stain. All illustrations were prepared from specimens in glycerin using a Wild microscope with camera lucida attachment. In addition to alizarin-stained material in glycerin, I found dried or alcoholic skeletal material easier to handle and extremely useful for quick reference if studied with discretion.

All of the study material is housed in the Division of Systematic Biology at Stanford University, except for the specimen of *Piaractus nigripinnis*, which was borrowed from the Department of Ichthyology of the California Academy of Sciences. Except when stated otherwise, the material represents alizarin preparations kept in glycerin. The lengths given in millimeters are standard lengths. In some instances an approximation of the standard length was determined from dried skeletal material.

The following skeletal material was examined:

Acestrorhynchus species: SU 59027, two specimens 50 and 57 mm. Brazil, Rio Negro at Cucuhy, at Colombian border, 14 February 1925, Carl Ternetz.—SU 39269, two specimens 44 and 58 mm. Brazil, Amazon at Teffé, 1865, L. Agassiz (note: all of my osteological figures of *Acestrorhynchus* are based on the smaller of these two specimens. Mr. Naercio Menezes has identified a specimen from the same series as belonging to a new species which is close to *A. nasutus*).—SU 2241, approximately 160 mm., dry skeleton. Brazil, C. F. Hartt.

Alestes baremose: uncataloged, three specimens 53–56 mm. Ghana, Volta River, 1963, T. Roberts.

Alestes grandisquamis (Boulenger): SU 48084, approximately 220 mm. Belgian Congo, Faradje, 1909–1915, American Museum of Natural History Congo Expedition.

Alestes imberi Peters: SU 36028, incomplete alcoholic skeleton prepared by G. S. Myers, total length of cranium 20 mm. Congo River.

Alestes liebrechtsii Boulenger: SU 48083, approximately 280 mm., dry skeleton. Belgian Congo, Faradje, 1909–1915, American Museum of Natural History Congo Expedition.

Anostomus species: uncataloged, aquarium specimen 47.8 mm.

Boulengerella cuvieri (Agassiz): SU 51052, one nearly complete dry skeleton and a partially disarticulated cranium, total cranial lengths 54 and 70 mm. Brazil, Amazon at Belém-do-Pará, 1911, E. C. Starks.

Brycon oligolepis Regan: SU 48082, approximately 170 mm., dry skeleton prepared by G. S. Myers. Colombia, Rio Dagua, 1913, C. H. Eigenmann.

Chalceus erythrus (Cope): SU 36871, 80 mm., stained and dissected cranium in alcohol. Peru, Tuye Caño near Pebas, 28 August 1936, W. G. Scherer.

Chilodus species: uncataloged, two aquarium specimens, 47 and 57 mm.

Citharinus congicus Boulenger: SU 51054, approximately 232 mm., dry skeleton. Belgian Congo, Congo River at Stanleyville Falls, 1909–1915, American Museum of Natural History Congo Expedition.

Congocharax olbrechtsi Poll: SU 63378, 22.5 mm. Congo (Leo), Ikabo River about 60 km. south of Coquilhatville, 8 August 1964, T. Roberts.

Ctenolucius hujeta (Valenciennes): SU 50392, two specimens 100 and 111 mm. Colombia, Magdalena basin, at or near the junction of the Rio Samana and the Rio La Miel, near La Dorada, 27 February 1957, Gen. T. D. White and Col. J. N. Reynolds.

Curimatus isognathus Eigenmann and Eigenmann: SU 54034, dry skeleton approximately 110 mm. Brazil, C. F. Hartt.

Distichodus fasciolatus Boulenger: SU 35095, approximately 435 mm., dry skeleton. Belgian Congo, Faradje, 1909–1915, American Museum of Natural History Congo Expedition.—Uncataloged, two specimens 14 and 18 mm. Congo, Congo River at Leopoldville, 9 November 1963, T. Roberts.

Hepsetus odoc (Bloch): uncataloged, two specimens 19 and 22.5 mm. Ghana, Tano River at Elubo, 25–30 June 1963, T. Roberts.—SU 47717, 42 mm. Cameroun, Lokunje River near Bipindi, 10–14 February 1963, Rev. A. I. Good.—SU 15770, 58.5 mm. Cameroun, Asok River (Mbotto basin), Rev. A. I. Good.—SU 47568, 94 mm. Cameroun, Mfiande and Seng Rivers, Ntem or Campo basin, November–December 1935, Rev. A. I. Good.—Uncataloged, approximately 200 mm., dry skeleton. Ghana, Ofin River near Dunkwa, May 1963, J. Emomidue.

Hoplias species: SU 53784, 20 mm. Colombia, Cordillera Macarena, Rio Guayabero below El Refugio, 24 February 1960, Gen. T. D. White and G. S. Myers.—Uncataloged, four specimens 36.5–58 mm. Venezuela, Rio Puctual, Rio Aragua basin, F. F. Bond.—SU 59466, 70 mm. Peru, Rio Ambiyacu, 4 September 1940, W. G. Scherer.—SU 3106, dry skeleton, total cranial length 31 mm. Brazil, Rio Tocantins at Marajó, C. F. Hartt.

Hydrocymus lineatus Bleeker: SU 48081, approximately 180 mm., dry skeleton. Belgian Congo, Congo River at Stanley Falls, 1909–1915, American Museum of Natural History Congo Expedition.

Hydrocynus species: uncataloged, several specimens about 20–30 mm., Ghana, Volta River at Amedica, 8–9 March 1963, T. Roberts.

Hydrolycus pectoralis (Günther): SU 48087, approximately 171 mm., dry skeleton. Brazil, mouth of Rio Madeira, Amazon basin, 1911, F. Baker and W. M. Mann.

Iguanodectes spilurus (Günther): uncataloged, aquarium specimen perhaps 75 mm., which disintegrated in potassium hydroxide after preliminary examination.

Leporinus fasciatus (Bloch): SU 22066, incomplete dry skeleton, cranium 40.5 mm. in total length. Brazil, Amazon at Belém-do-Pará, 1911, E. C. Starks.

Mesoborus crocodilus Pellegrin: SU 51055, approximately 228 mm., dry skeleton. Belgian Congo, Poko, 1909–1915, American Museum of Natural History Congo Expedition.

Micralestes occidentalis (Günther): SU 62846, numerous specimens 40–60 mm. Ghana, Birrim River near Kade, 31 December 1962, T. Roberts.

Mylossoma species: SU 48085, approximately 115 mm., dry skeleton. Brazil, Rio Madeira.

Phenacogrammus interruptus (Boulenger): SU 64556, 40 mm. Congo, Congo River at Leopoldville, 9 November 1963, T. Roberts.

Piaractus nigripinnis (Cope): CAS 24031, 528 mm., dry skeleton prepared by J. D. Hopkirk. Brazil, Amazon.

Rhaphiodon vulpinus Agassiz: SU 48086, approximately 260 mm., dry skeleton. Brazil, Amazon at Belém-do-Pará, 1911, E. C. Starks.

Roeboides guatemalensis (Günther): SU 24757, four specimens 33–58 mm. Panama, Gatun Lake, 23 March 1930, Zschokke and Blackwelder.

Salminus brasiliensis (Cuvier): SU 31615, 212 mm. Buenos Aires, A. W. Herre. Originally an alizarin preparation in glycerin, transferred to alcohol after defleshing by hand.

Schizodon fasciatus (Spix): SU 36938, 47 mm. Peru, Shansho Cano near Pebas, 28 July 1937, W. G. Scherer.

Serrasalmus “*piraya*” (probably *S. nattereri* Kner): SU 2350, approximately 120 mm. Brazil, lower Amazon, C. F. Hartt.

Xenocharax spilurus Günther: SU 64472, 40 mm. Congo, Congo River at Coquilhatville, 9 August 1964, T. Roberts.

The sequence in which the figures are presented and the layout of the subject matter in the figures, with minor modifications, is the same as in the works on characoid osteology by Weitzman (1954, 1962, 1964) and Roberts (1966). Unless stated otherwise in the legends, the figures of each species are based on a single specimen, as follows:

Hepsetus odoe: SU 47568, 94 mm.

Ctenolucius hujeta: SU 50392, 100 mm.

Hoplias species: uncataloged, 58 mm.

Salminus brasiliensis: SU 31615, 212 mm.

Acestrorhynchus species: SU 39269, 44 mm.

OBSERVATIONS

CRANIUM

ETHMOID REGION. In most teleosts, as noted by Sagemehl (1885, pp. 30-31), the ethmoid bone is restricted to the skull roof, whereas in characoids it generally also takes part in forming the internasal septum and has a posterior portion underlying the anterior part of the frontal bones.

In primitive or generalized characoids and also in some highly specialized ones (including *Hepsetus*, *Ctenolucius*, *Hoplias*, *Salminus*, and *Acestrorhynchus*) the ethmoid bone ends anteriorly in a well developed conic process or spine which projects between the paired premaxillaries to the tip of the snout or almost to the tip, thus entirely or largely preventing the premaxillaries from contacting each other in the midline. Judging from the genera having an anterior ethmoid spine and from its usual association with generalized jaw structure, it is a primitive feature of characoids.

In *Hoplias* the premaxillaries are entirely prevented from contacting each other by the ethmoid spine, which extends to the very tip of the snout. According to Starks (1926, p. 159) the premaxillaries do come in contact anterior to the ethmoid spine in *Hoplias malabaricus*; I have, however, re-examined the 36-mm. skull of *Hoplias malabaricus* (cataloged as SU 3106) that Starks studied. The premaxillaries have been separated from the cranium in this specimen, and were presumably separate at the time of Stark's examination. After placing them in position it is evident that normally they would have been not at all or perhaps just barely in contact anterior to the ethmoid spine. In *Hepsetus* and *Ctenolucius*, on the other hand, although the ethmoid spine is notably elongate it does not reach the snout-tip, which is formed by the premaxillaries, and the premaxillaries meet in the midline for a considerable distance anterior to the ethmoid spine (figs. 6, 7). In many specialized characoids the ethmoid spine is wanting. In such instances the premaxillaries usually meet in the midline and are ligamentously or suturally united.

Hoplias, *Salminus*, and *Acestrorhynchus* have a lateral ethmoid wing (as in *Brycon*) to which the upper limb of the maxillary bone is ligamentously attached. This lateral wing is absent in *Hepsetus* and *Ctenolucius*.

Ventrally the characoid ethmoid bone articulates with the vomer, which in turn articulates with the anterior shaft of the parasphenoid bone. In *Hoplias*, *Salminus*, and *Ctenolucius* the ethmoid and the vomer unite by a more or less straight, transverse suture; in *Hepsetus* and large specimens of *Acestrorhynchus*, however, the suture between these two bones is strongly interdigitating.

In many characoids the anterior ends of the ectopterygoids are attached by slender ligaments to the ventral surface of the vomer. In *Hepsetus* the sides of the vomer where these ligaments attach are deeply excavated (fig. 16). In *Ctenolucius*, in contrast, the ligaments attach to a pair of slight, rounded prominences on the posteroventral surface of the vomer (fig. 17).

RHINOSPHEOID. The rhinosphenoid is a plate-like median bone in the interorbital septum in some characoids. Its anterior portion lies between the paired lateral ethmoids; its posterior portion extends nearly to the orbitosphenoid, and may contact the latter bone in some instances. This bone has not been reported in any other group of fishes (Weitzman, 1962, p. 44). Within the characoids its occurrence is apparently restricted to the family Cynodontidae (verified in *Rhaphiodon* and *Hydrolycus*), and to American members of the family Characidae in which the portion of the parasphenoid lying ventromedially to the orbits is remote from the orbitosphenoid bone. The orbitosphenoid is in more or less intimate contact with the parasphenoid in minnows, catfishes, and many non-characid characoids, including Erythrinidae, Anostomidae, Lebiasinidae, Hepsetidae, and Ctenoluciidae, as well as in the primitive characid *Salminus*. This condition is undoubtedly primitive for characoids.

In *Hepsetus* the entire ventral edge of the orbitosphenoid lies on the parasphenoid and the parasphenoid has a dorsally-projecting process sutured to the posteroventral portion of the orbitosphenoid (fig. 11). In *Salminus* the orbitosphenoid is in contact with the parasphenoid by a narrow endochondral joint and the rhinosphenoid is absent. Nevertheless, the orbitosphenoid and parasphenoid are fairly widely separated for most of their lengths (fig. 14). In this respect *Salminus* is intermediate between, on the one hand, primitive characoids lacking the rhinosphenoid (in which the orbitosphenoid and parasphenoid are usually intimately connected) and, on the other hand, some of the more specialized Characidae with a rhinosphenoid (in which the orbitosphenoid and parasphenoid are remote from each other). *Roeboides guatemalensis*, *Iguanodectes*, and *Acestrorhynchus* (fig. 15) have very large rhinosphenoids.

PARASPHEOID. In most characoids the portion of the parasphenoid ventromedial to the orbits is straight, but in many members of the family Characidae, including *Alestes* and *Brycon*, it is more or less strongly depressed ventralwards. This is apparently a specialized feature. *Salminus* is somewhat intermediate in this respect between most characids and primitive characoids, such as *Hepsetus* and *Erythrinus*, in which the parasphenoid is straight for its entire length.

In *Hoplias* and *Hepsetus*, and in some specialized characoids, there is a median ridge projecting ventrally from the parasphenoid, extending from the lateral wings of the parasphenoid anteriorly to the point where the parasphenoid meets the vomer. This ridge is reduced or entirely absent in a few specialized characoids (e.g., *Mesoborus*). It is not present in the minnow *Opsariichthys*.

In *Hepsetus* and *Leporinus* it is continuous with a ridge extending on the ventral surface of the vomer.

CRANIAL SCULPTURING. Sagemehl (1885) was particularly impressed by the similar sculpturing of cranial roofing bones in *Hepsetus*, *Erythrinus*, and *Amia*, and Gregory and Conrad (1938) noted cranial sculpturing in *Hoplias*, *Ctenolucius*, and *Hepsetus*. The cranial roofing bones are highly sculptured in still other characoids, including *Piaractus*, *Salminus*, and *Phago*. In all of these fishes the jaw bones, circumorbital and opercular series of bones, pterotics, parietals, frontals, and even the ethmoid bone bear numerous striae and sulci, or ridges and grooves, on their exposed surfaces. The striae tend to lie parallel on elongate bones like the jaws and frontals, but are more irregularly arranged on some of the other bones.

In characins, as well as catfishes with sculptured cranial bones, the integument covering the skull is usually very thin, as in *Amia*. The thickness of the skin overlying the skull bones varies considerably in characoids, in some instances even between closely related species. According to Monod (1950, p. 47), two groups of *Alestes* can be distinguished partly on the basis of the relative thickness of their cranial integument. He cited *A. dentex* and *A. baremose*, which have a very thin integument, and *A. nurse* and *A. macrolepidotus*, which have a very thick, fatty integument. In this instance the thin cranial integument is not accompanied by cranial sculpturing.

Cranial sculpturing seems to be characteristic of many large ostariophysans, including large catostomids, minnows (especially carp types), and catfishes, as well as characoids. It has probably arisen independently in diverse groups of characoids.

CRANIAL FONTANELS. AS Regan (1911, p. 17) stated, the presence or absence of fontanel in [adult] characoids is probably sometimes a primitive feature, sometimes not. Regan regarded the condition of the fontanel as of negligible taxonomic importance and cited a number of characoids with closed fontanel which are closely related to species in which the fontanel remain open. Fontanel are apparently present in the young of all characoids. As noted by Regan, the fontanel are usually closed in the adults of characoids which have a dorsally flattened cranium and low occipital crest. *Hepsetus*, *Ctenolucius*, and *Hoplias* fall in this category. Sagemehl (1885) regarded the absence of cranial fontanel in *Hepsetus* and *Erythrinus* as a primitive feature. The fontanel in a 212-mm. specimen of *Salminus* are narrow and the anterior fontanel ends slightly anterior to the epiphyseal bar which separates it from the posterior fontanel (fig. 9). In very large specimens of *Salminus* the fontanel are lacking. In *Acestrorhynchus* the cranial fontanel persist in the adults and are rather large (fig. 10).

EPIPHYSEAL BAR. The epiphyseal bar serves for attachment of the epiphysis.

In characoids with a longitudinal dorsal cranial fissure it separates the anterior and posterior fontanels from each other. The epiphyseal bar is probably a developmental feature of all characoids, including those in which the cranium becomes completely roofed over. It has been described in the developing chondrocranium of *Hepsetus* by Bertmar (1959). The epiphyseal bar usually becomes ossified in characoids, at least in those with cranial fontanels. According to Sagemehl (1885), it remains cartilaginous in *Hoplerythrinus unitaeniatus* and *Citharinus geoffroyi*. I find it well ossified in a large specimen of *Citharinus congicus* (SU 51054). In many primitive or generalized characoids, including *Salminus*, *Hepsetus*, *Hoplías*, and *Brycon* (Weitzman, 1962, fig. 2, p. 58), and also in *Distichodus*, *Curimatus*, and *Acetrorhynchus* (fig. 10), the epiphyseal bar is represented in adults by a narrow osseous span across the longitudinal cranial fissure. In some specialized characoids, however, including *Serrasalmus*, *Mylossoma*, *Rhaphiodon*, and *Hydrolycus*, and also in the gymnotoid *Sternopygus*, the transverse bony bar separating the anterior and posterior fontanels is notably wider. This widening is apparently due to an encroachment of dermal ossification from the frontal bone onto the original endochondral ossification of the epiphyseal bar, and should be regarded as a specialization.

In a large specimen of *Hepsetus* in which the cranial fontanels are completely roofed over by the frontal and parietal bones, the epiphyseal bar is represented by a narrow, bony, transverse ridge on the ventral surface of the frontal bones inside the cranial cavity. In *Hoplías*, on the other hand, the ventral intracranial surface of the frontal bones is smooth in the corresponding region, and there is no indication of an ossified epiphyseal bar in a relatively small specimen in which the fontanels have become closed.

LATERAL MARGIN OF THE CRANIAL ROOF. A flattened or slightly vaulted cranial roof in which the dorsolateral margin is more or less straight, as in Erythrinidae, Hepsetidae, and Ctenoluciidae, is probably a primitive feature of characoids. This condition is approached in *Salminus*. In *Brycon*, as in most characoids, the evenness of the dorsolateral margin of the skull is broken by the dilator groove. Many of the deeper-bodied characoids, such as *Citharinus* and *Serrasalmus*, are characterized by broad-based, laterally projecting processes of the frontal bone, which form part of the posterior wall of the orbit, and by extension of the dilator groove onto the dorsal portion of the skull. There is a very general tendency in specialized characoids for the cranial roof to be highly vaulted and for the frontal bone to have lateral processes or fossae interrupting the even contour of the dorsolateral skull margin (Sagemehl, 1885, p. 28).

SPHENOTIC BONE AND DILATOR GROOVE. As observed by Sagemehl (1885, p. 32), in most characoids a well developed fossa extends from the sphenotic spine onto the skull roof. This fossa, known as the dilator groove, serves for attachment of the *m. dilator operculi*. Sagemehl stated that it is not developed in

Hepsetus and in the Erythrinidae, and that it is but weakly developed in *Anacyrtus* [= *Charax*]. Sagemehl's comments on the sphenotic bone and dilator groove seem important enough to be reproduced here (with minor paraphrasing):

The characoid sphenotic has approximately the form of a three-sided pyramid, the anterior and dorsal surfaces of which are directed laterally and ventrally and against the orbit. The dorsal surfaces of the sphenotic, which in *Amia* takes part in the formation of the skull roof and bears the characteristic sculpturing of the membrane bones of the cranial roof, has moved deeply beneath the surface of the skull. This displacement has been conditioned by the differentiation of a new muscle out of the common mass of the original *m. levator palatii*, the *m. dilator operculi*. This muscle is lacking in *Amia* and in the rest of the bony ganoids. In most characoids and in the majority of bony fishes it takes its origin from the dorsal surface of the sphenotic and the part of the frontal bordering the sphenotic. It is strongly developed in most characoids, and has a separate muscle fossa which is enclosed anteriorly and medially by sharp rims and which occupies the entire dorsal surface of the sphenotic process. The genera *Hoplerythrinus* and *Hoplias* [Sagemehl's *Erythrinus* and *Macrodon*] deviate from other characoids in that the *m. dilator operculi* takes its origin only in the orbit, and in order to reach the dorsoanterior edge of the opercle it passes through a short but wide canal which arises by a separating from each other of the sphenotic and of the overlying frontal. In *Hepsetus*, on the other hand, there is only a slight indentation between the frontal and the posterior part of the sphenotic (Sagemehl, pp. 61, 62).

According to Allis (1897, pp. 557-558), the *m. dilator operculi* is present as a separate muscle in *Amia*. It lies above and in close contact with the *m. levator arcus palatini*, but has no connection with the latter except at its origin. It arises from the entire lateral edge of the pterotic [= squamosal of Allis] back as far as the upper end of the preopercle, and from the sphenotic spine [= post-orbital process] behind and above the origin of the *m. levator arcus palatini*. The surface of origin of the two muscles at this place is continuous, but the muscles themselves are markedly distinct and separate.

The conditions for the insertion of the *m. dilator operculi* in Erythrinidae are peculiar, and it is not clear whether this insertion is primitive or specialized. A similar canal between the sphenotic and frontal bones is present in *Ctenolucius* and *Boulengerella*, and presumably it has the same significance as in Erythrinidae. In Erythrinidae and Ctenoluciidae the sphenotic spine is very small. In Erythrinidae it does not extend beyond the lateral margin of the skull at all. In Ctenoluciidae it extends beyond the lateral margin slightly, but is relatively much smaller than in *Hepsetus* and most other characoids.

It is perhaps incorrect to say that a dilator groove is lacking in *Hepsetus*. As noted by Sagemehl, there is an indentation between the frontal and the pos-

terior portion of the sphenotic; the recess formed there is moderately deep and is equivalent to the dilator groove. A similar but deeper dilator groove is present in *Leporinus*.

The form of the dilator groove in *Brycon* is typical of that found in Characidae. The frontal is strongly indented where it overlies the sphenotic and the indentation provides a sharp dorsal rim for the dilator groove. The dilator groove is roofed over by the sixth infraorbital. The dilator groove in *Alestes* and *Hydrocynus* is similar to that in *Brycon*.

In *Salminus* the dilator groove is exceptionally long and extends on the ventral surface of the frontal anteriorly to the middle of the orbital roof (fig. 19). This unusual condition is not met with in any other characid I have examined. One consequence of this condition is that the lateral margin of the skull of *Salminus* is straighter and perhaps more primitive in this respect than it is in characids in which the dorsal surface of the skull has been invaded by the dilator groove.

In *Acestrorhynchus* there is a large passageway between the sphenotic and the frontal. The sphenotic spine extends far laterad to the lateral edge of the frontal except for a strut-like process from the frontal which forms a bridge out to the tip of the sphenotic spine, with which it fuses (fig. 10). The passageway or canal thus formed differs somewhat in appearance from the sphenotic-frontal canals in Erythrinidae and Ctenoluciidae but may be similar in function to the latter structures.

In *Citharinus* and *Distichodus* the dilator groove is broad and deep, and extends far onto the skull roof. The frontal wing serving as the anterior shelf of the dilator groove projects prominently from the side of the skull as a broadly based triangular spine unconnected to the sphenotic spine. This condition is probably highly specialized. In *Serrasalmus* the dilator groove is similar to that in *Citharinus* but the sphenotic spine extends strut-like to the tip of the corresponding frontal spine with which it fuses to form a broad canal or passage opening into the orbit.

In *Rhaphiodon* there is a peculiar fossa in the roof of the orbit which originates in front of the base of the sphenotic spine and ends anteriorly in a recess between the orbitosphenoid and the frontal bones. *Hydrolycus* has a similar groove except that it is shorter and broadly open anteriorly. These structures are probably dilator grooves.

PARIETAL BONES. The most primitive condition of the parietal bones in characoids is probably found in the Erythrinidae, Ctenoluciidae, and Hepsetidae. In adults of these families the median edges of the left and right parietals meet in the midline and are suturally united for their entire lengths. Thus the posterior portion of the cranial fontanel is closed, and the supraoccipital bone is excluded from the roof of the skull and from the posterior cranial margin. Two

additional primitive features are associated with these conditions. First, the left and right supratemporal branches of the cephalic lateral line (which are enclosed in transverse bony canals near the posterior margins of the parietal bones) meet each other in the dorsal midline, where they open to the surface through a common median pore. Second, the origin of the scale rows on the dorsal surface of the body is not interrupted by the supraoccipital crest, but is parallel with the posterior margin of the parietals. The forward edges of the anteriormost scales in the dorsal scale rows insert in a groove in the parietal bones which lie immediately ventral to the posterior margin of the cranial roof.

SUPRAOCCIPITAL BONE. In most characoids the median supraoccipital bone forms the posterior border of the frontal fontanel and has a dorsal groove, the supraoccipital sulcus, extending from the posterior edge of the fontanel to near the tip of the supraoccipital spine. As remarked by Sagemehl (1885, p. 28) the supraoccipital spine attains larger sizes in characoids than in any other of the lower teleosts. The deep-bodied pacús of the genus *Myleus* have a notably large supraoccipital spine. According to Alexander (1965, p. 176), it provides a firm origin for the high dorsal epaxial muscles, and its base has lengthened and extends further forward on the skull than in generalized characoids in order to be strong enough to withstand the torques applied to it by the alternate contraction of the contralateral muscles. The supraoccipital spine is similarly modified in some other deep-bodied characoids including *Citharinus*.

As noted by Sagemehl (1885, p. 46), the supraoccipital spine in Erythrinidae and in *Hepsetus* is considerably smaller than is usual for characoids. This is also true of *Ctenolucius*. In adults of these fishes the supraoccipital bone does not form the posterior border of the cranial fontanel, since there is no cranial fontanel, and there is no indication whatever of a dorsal supraoccipital sulcus. It may be noted that the supraoccipital spine and sulcus are well developed in both *Mesoborus* and *Hydrocynus*. In adults of these genera the cranial fontanel is completely closed, but they both are clearly descended from fishes in which the fontanels were present.

Weitzman (personal communication) suggests that perhaps no major phyletic significance can be attached to the crest, it just being a function of body shape. In general, cylindrical characoids (e.g., lebiasinids and erythrinids) have a short supraoccipital crest, deep-bodied ones a prominent crest.

NOTE ON SQUAMATION ON THE HEAD. The presence or absence of scales on the head is a taxonomically important character at various levels in the classification of fishes. In characoids and cyprinids squamation never extends onto the head; in other words, the cranial roof and the facial bones of the skull are devoid of scales in all characins and minnows (in this connection it is interesting that the body plates of some catfishes, which may or may not be derived from scales, never extend onto the head). Some cobitids have head scales, a strange special-

ization for an ostariophysan (Weitzman, personal communication). Many acanthopterygians and some lower teleosts (e.g., *Esox*, *Gonorhynchus*, cyprinodonts) have the head more or less extensively covered by scales.

In *Hepsetus*, *Ctenolucius*, and in *Hoplias* and other members of the Erythrinidae, the anteriormost scales of all of the dorsal scale rows are inserted in a groove along the posterior edge of the parietal bones, and the supraoccipital spine is completely covered by scales. This mode of insertion of the dorsal scale rows is perhaps primitive for characoids. In characoids in which the supraoccipital bone has a strongly developed crest the dorsomedian scale rows are interrupted by the crest and insert on either side of it instead of directly on the parietal; thus the supraoccipital bone is exposed on the ridge of the nape, or rather is covered only by a more or less thin, scaleless layer of skin. The relationship of the scales to the crest is related to the size of the crest, which in turn is correlated with body shape. Cylindrical or subcylindrical body shape may well be primitive in characoids. Similar modes of insertion of the scales on the nape may have secondarily developed along with cylindrical body shape in other characoids.

SLOPE OF THE OCCIPUT. Sagemehl regarded the sloping inclination of the occiput in Erythrinidae as a primitive condition comparable with the slope of the occiput in *Amia*, and unlike that in any other characoids. In Erythrinidae the supraoccipital spine is far anterior to the basioccipital centrum. It is noteworthy that the occiput slopes similarly in the primitive minnow *Opsariichthys*. In specialized characoids the supraoccipital spine lies more or less directly above the basioccipital centrum and the occiput is practically vertical.

In *Chalceus* and *Pyrhulina* (members of the family Lebiasinidae) the occipital slope is fully comparable to that of Erythrinidae, and that of *Ctenolucius* and *Hepsetus* nearly so. Therefore Sagemehl was incorrect in stressing the uniqueness of the erythrinids in this respect. Weitzman discussed the osteology and relationships of the Lebiasinidae with regard to the Erythrinidae and concluded that in all the unique respects that the latter differ from the Characidae, the Lebiasinidae are like the Characidae (Weitzman, 1964, p. 155). He did not compare their occipital regions. Weitzman (personal communication) suggests that the slope of the occiput might be correlated with body shape.

POSTTEMPORAL FOSSAE. As indicated by Sagemehl (1885, pp. 28, 29), large posttemporal fossae (which serve for cranial attachment of epaxial musculature) are characteristic of characoids. There is considerable variation among specialized characoids regarding the nature of the openings into these fossae. In the primitive or generalized characoids, however, including Erythrinidae, Hepsetidae, Ctenoluciidae, *Brycon*, and *Salminus* (and also in some specialized characoids such as *Leporinus*), the openings show remarkably little variation. In all of these fishes there is an oblique or nearly horizontal dorsal opening, the mar-

gins of which are formed by portions of the parietal, epiotic, and supraoccipital bones, and a larger, ventrolateral vertical opening, the margins of which are formed by portions of the pterotic and epiotic bones.

In the specialized characoids *Distichodus*, *Mesoborus*, and *Hydrolycus*, in addition to the two openings just mentioned, there is a third opening between the epiotic and exoccipital bones mesad to the ventrolateral vertical opening, which is separated from the latter by the portion of the epiotic forming a bony canal around one of the membranous vertical semicircular canals. In *Citharinus* (Sagemehl, pl. 2, fig. 5) the ventrolateral and ventromedial openings into the posttemporal fossa seem very similar to these openings in *Distichodus*, but the dorsal opening present in primitive characoids is absent; the area between the epiotic, supraoccipital, and parietal bones is solid bone.

Curimatus isognathus, *Alestes liebrechtsii*, and *Hydrocynus* (Sagemehl, pl. 3, fig. 16) have three openings into the posttemporal fossa, as in *Distichodus*, *Mesoborus*, and *Hydrolycus*, but the ventromedial vertical opening lies entirely within the epiotic bone, i.e., the exoccipital does not contribute to its margin. In *A. liebrechtsii* the openings into the posttemporal fossae are exceptionally large and the portions of the epiotic bone separating them are extremely slender. A similar condition is met with in the gymnotoid *Sternopygus*. *Alestes* (*Brycinus*) *grandisquamis* resembles *A. liebrechtsii* in that the dorsal oblique and ventrolateral vertical openings are extremely large and the portion of the epiotic separating them is extremely slender, but the ventromedial opening found in the latter species is lacking. *Acestrorhynchus* has an exceptionally large ventrolateral vertical opening in the posttemporal fossa; other openings are lacking (fig. 25). This condition is undoubtedly highly specialized.

SUBTEMPORAL FOSSA. Weitzman (1962, p. 26) reported that in *Brycon meeki* the subtemporal fossa is represented by a shallow depression in the posterior region of the prootic which extends backward to the region of the suture between the prootic, pterotic, and basioccipital. He noted the presence of an extremely shallow subtemporal fossa in gasteropelecids, and stated that *Hoplias malabaricus* has a [relatively] well developed subtemporal fossa. Ridewood (1904, p. 62) remarked that this fossa is unrecognizable in the majority of characoids; with the exception of *Citharinus* and *Serrasalmus*, however, the subtemporal fossa is clearly distinguishable in all of the characoids I have examined. Besides *Hoplias*, it is relatively well developed in *Hepsetus*, *Ctenolucius*, *Acestrorhynchus*, and *Distichodus*. In *Hydrolycus* it is exceptionally broad but very shallow. In *Salminus* and *Alestes* it is similar to that of *B. meeki*.

Note: Catfishes characteristically lack subtemporal fossae, the prootic and adjoining bones tending to present a smooth and slightly convex surface in all catfishes, whereas minnows have larger and deeper subtemporal fossae than any other teleosts.

INTERCALAR BONE. The intercalar (sometimes called opisthotic) is a thin bone which is closely applied to adjacent portions of the prootic, exoccipital, and basioccipital bones. It overlies a substantial portion of the joint between the basioccipital and exoccipital. The intercalar is well developed in *Hepsetus*, *Ctenolucius*, *Hoplías*, *Salminus*, and *Acestrorhynchus*. In all of them a strong ligament originates from it and attaches to the prong-like lower limb of the post-temporal bone of the secondary pectoral girdle.

In glycerin specimens the translucency of the intercalar sometimes makes it difficult to distinguish from the underlying bones. Because of this the intercalar is not well portrayed in my figures of *Hepsetus*, *Ctenolucius*, and *Hoplías*. It is best shown in figures 14, 19, and 24 of *Salminus*. It is relatively easy to observe the intercalar in specimens that have been transferred from glycerin to alcohol. One can then observe the specimen in alcohol or allow it to dry a bit and readily make out the intercalar.

JAWS

GENERAL FEATURES. In primitive and generalized characoids the jaws are shaped like those of *Amia*, although there is a tendency for the posterior portion of the maxillary to extend beyond the gape. In many characoids the posterior portion of the maxillary slips under the ventral rim of the first infraorbital bone. In generalized characoids the premaxillaries are immovably fixed to the skull. It should be noted that primitive teleosts of several groups have relatively non-movable premaxillaries, e.g., osmerids (Weitzman, 1967). The ascending limb of the maxillary is a slender, toothless process movably articulated to the vomer and to the posterior edge of the premaxillary. The descending limb is an expanded, tooth-bearing lamella bound by a ligament to the posteromedial surface of the lower jaw. When the mouth is closed this ligament lies folded in the rictus of the jaws. As the mouth is opened it unfolds and then pulls the descending limb of the maxillary forward. The maxillary must come forward to permit full depression of the lower jaw.

Salminus, *Hepsetus*, *Hoplías*, and *Acestrorhynchus* have generalized jaws. In *Ctenolucius*, although the dentition and replacement tooth trenches appear to be primitive (Roberts, 1967a), the premaxillaries are exceptionally elongate, almost completely excluding the maxillaries from the gape, and the maxillaries are immovably fused to the premaxillaries. This is a highly specialized condition.

Weitzman (1960a, p. 118) briefly discussed some characoids in which the maxillary is excluded or nearly excluded from the gape. The American characoids in his discussion—*Serrasalmus*, *Mylossoma*, *Poecilobrycon*, and *Nannostomus*—have foreshortened rather than elongated jaws. The African Ichthyboridae mentioned, on the other hand, tend to have elongate jaws. Two of the

genera, *Belonophago* and *Gavialocharax*, have jaws fully elongate as those of *Ctenolucius* and *Boulengerella*. *Gavialocharax*, incidentally, is apparently closely related to *Phagoborus*, differing most strikingly from the latter in the more elongate form of its jaws. In ichthyborids the maxillary, which never bears teeth, is almost entirely fused to the medial face of the posteriormost parts of the premaxillary. The premaxillary is movably articulated to the skull and swings upward when the lower jaw is fully depressed.

In characoids, as pointed out by Rowntree (1906, p. 243), all intermediate stages are found between, on the one hand, the presumably primitive condition in which the maxilla bears teeth throughout its length and forms the major part of the border of the mouth, and, on the other, the condition in which the maxilla is toothless and so reduced as to be practically excluded from the gape.

A movable premaxillary would appear to be highly specialized for characoids. This condition occurs in several of the specialized characoids, including ichthyborids, *Bivibranchia*, and *Hydrocynus*. In *Hydrocynus* the maxillary is fused to the premaxillary and does not bear teeth.

The relationship of the posterior portion of the maxillary bone to the first and second circumorbital bones exhibits important differences in characoids. When the jaws are closed the portion of the maxillary bone extending posterior to the gape of the mouth is entirely or almost entirely overlain by the first and second circumorbitals in *Hepsetus* (fig. 1), *Ctenolucius* (fig. 2), *Acestrorhamphus* and *Salminus* (fig. 4). In *Acestrorhynchus* the first circumorbital is ventrally prolonged to form a scabbard-like sheath which overlies the maxillary, and the second circumorbital is thus excluded from overlying the maxillary (fig. 5). In *Brycon*, as in many characoids, the posterior portion of the maxillary is partially overlain by the first and second circumorbitals. Weitzman (1964, p. 142) stated that in *Hoplias* the fan-shaped distal end of the maxillary is external to the second circumorbital, but that it is included under the second circumorbital in *Hoplerythrinus* and *Erythrinus*. It is probable that the distal end of the maxillary normally slips beneath the second circumorbital in all Erythrinidae including *Hoplias*, as shown in figure 3. When the mouth of a preserved specimen of *Hoplias* is forced open, it usually shuts with the maxillaries in an abnormal position outside the second circumorbital; with a slight manipulation, they can be guided into their normal position inside the second circumorbital. I doubt that live *Hoplias* individuals ever close their mouths in such a way that the maxillary lies outside the circumorbital bone, but this should be verified by observations on living fishes. In Erythrinidae the first circumorbital bone is reduced to a bony canal enclosing a portion of the circumorbital branch of the cephalic lateral line; hence it lacks the lamellar portion which would normally overlap the maxillary bone. In many characoids, as in *Lepidarchus* (Roberts, 1966, fig. 1), the first and second circumorbitals are so greatly reduced that neither of them

overlies the maxillary. In *Genycharax* (Géry, 1966, fig. 12) and *Lonchogenys* the first circumorbital overlies the maxillary to a considerable extent, but the second circumorbital is reduced and the posteriormost portion of the maxillary lies entirely exposed. The greatly expanded, otter-board-like maxillaries of *Thriassobrycon* lie completely outside the circumorbitals (Böhlke, 1953, fig. 1).

Géry (1963a, p. 278, fig. 7) described a supramaxillary bone sutured to the maxillary in *Agoniates*. Hitherto this element had not been reported in any characoid. A small, separate element apparently equivalent to a supramaxillary is also present in some species of *Chilodus*. In *Chalceus* the posterior portion of the maxillary is grooved in such a way as to suggest that its dorsoposterior portion is actually a fused supramaxillary bone. In *Hoplias*, the dorsoposterior portion of the maxillary has a dorsal flange in the region where the supramaxillary is present in *Amia*. This flange may represent a supramaxillary but examination of alizarin preparations of *Hoplias* of various sizes (including one 20-mm. specimen) failed to reveal a separate ossification or even a suture that might represent the line of fusion between maxillary and supramaxillary.

SYMPHYSEAL HINGE JOINT. A peculiar characteristic of almost all characoids is the complex hinge joint uniting the right and left halves of the lower jaw at the symphysis (Eastman, 1917; Gregory and Conrad, 1937, 1938; Alexander, 1965). In most characoids these facilitate lateral expansion of the mouth at the angle of the jaws, as Eastman (p. 757) first noted in *Hydrocynus* and *Hoplias*. The symphyseal hinge joint is particularly well developed in the elongate lower jaw of the characoid *Rhaphiodon*, which is highly specialized for killing and swallowing relatively large prey. Nelson (1949, pp. 505-506, pl. 4, figs. 6-8) gave the following account of the structural modifications permitting expansion of the lower jaw in this genus.

The bicipital articulations of the hyomandibular with the pterotic and sphenotic of the cranium is long and narrow allowing for the lateral swinging of the whole jaw suspension apparatus. Anteriorly the transverse articulation of the suprapterygoid [= palatine] with the pterothmoid [= ethmoid] allows lateral sliding and thus accommodation for the lateral swinging of the suspensory apparatus. The third articulation involved is that of the intermandibular (mental) [= symphyseal hinge joint of the lower jaw] whose "knuckles" allow a change in the angle of the mandibles from 0-60°. The sphenotic affords an origin for the levator arcus palatini which inserts upon the flat lateral surface of the hyomandibular. With the added lateral length of the sphenotic this muscle is given additional leverage for pulling the jaws laterally. The adductor arcus palatini muscle originates on the posterior portion of the parasphenoid and inserts upon the median surfaces of the pterygoid [= metapterygoid] and hyomandibular. Thus it has a direct pull to bring the jaws medially again.

Nelson also stated (in the explanation of pl. 4) that the hinge joint of *Rhaphiodon* is so highly interdigitated that it must be partially broken before the two halves of the jaws can be separated. In *Hoplias*, although the hinge

joint is fairly well developed, the two halves of the jaws can be separated readily without breakage.

In Ichthyboridae the lower jaws are so firmly sutured together at the symphysis that no lateral expansion is possible. In *Hydrocynus* the premaxillaries are movably articulated to the skull and they are joined together by a hinged joint like that present in the lower jaw (Eastman, 1917). Symphyseal hinge joints are absent in the highly specialized characoid *Anisitsia* of the family Hemiodontidae (Alexander, 1965, p. 187), and in the gymnotoids *Sternopygus* and *Electrophorus*.

SUSPENSORIUM AND PALATAL BONES

The mandibular and palatine arches of *Hepsetus*, *Ctenolucius*, *Hoplias*, *Acestrorhynchus*, and *Piaractus* are similar in their general plan to these structures in *Brycon mecki* as described by Weitzman (1962, p. 341, fig. 10, p. 66). All of them have a large metapterygoid-quadrate fenestra. As reported by Weitzman (1964, pp. 144, 148), this fenestra is lacking in the Lebiasinidae. It is also absent in *Leporinus* and *Rhaphiodon*. In the latter genus there is a thin, translucent sheet of bone between the metapterygoid and quadrate where the fenestra usually lies. In the related genus *Hydrolycus* the fenestra is present. Greenwood and others (1966, p. 385, fig. 9) reported a metapterygoid-quadrate fenestra in the primitive minnow *Opsariichthys* and in the closely related *Zacco*, and indicated that it may be a primitive feature for cyprinids and cyprinoids in general, although it is apparently absent in the majority of them.

In *Salminus* and *Acestrorhynchus* the hyomandibular has a process extending anteriorly along the dorsal edge of the metapterygoid until it meets the posterior end of the mesopterygoid (figs. 31, 32). This process is absent in other characoids examined.

In *Hoplias*, *Acestrorhynchus*, and *Ctenolucius* the ectopterygoid bears sharp conical teeth for the entire anterior two-thirds to three-quarters of its length. In *Salminus*, *Piaractus*, and *Hepsetus* the ectopterygoid is toothless.

In *Hoplias*, as noted by Sagemehl (1885, p. 95) and also by Weitzman (1964), there is a small, autogenous and movable tooth-bearing bone connected closely to the anterior end of the ectopterygoid (fig. 18). The interpretation of this element is of considerable interest because of the presence of similar tooth-bearing bones in *Amia* and in *Hepsetus* (reported below). As stated by Weitzman (1964, p. 146):

The accessory palatine of Sagemehl (1885, p. 95) that occurs in *Hoplias* may be interpreted in two ways, either as a dermopalatine or dental element that has not fused to the ectopterygoid or as an autogenous, anterior piece of the ectopterygoid. Starks (1926, p. 161) maintains that the accessory palatine is homologous with the dermopalatine of *Amia*. This problem cannot be resolved with the information at hand.

Weitzman also said that the striations and growth pattern of these tooth-bearing bones indicate that they are anterior extensions of the ectopterygoids.

Hepsetus has a large, tooth-bearing bone lying between the toothless ectopterygoid and the maxillary (figs. 16, 26). This element is not so closely connected to the ectopterygoid as is the accessory ectopterygoid of *Hoplias*. Günther (1864, p. 352) referred to it as a process of the intermaxillary [= premaxillary] bone, and Regan (1911, p. 16) perpetuated this error. The bone under consideration is definitely a separate element in every alizarin preparation of *Hepsetus* I have examined (specimens from 19 to 200 mm. in standard length). Apart from Erythrinidae, a comparable element has not been found in any other characoids. The presence of this bone in *Hepsetus* forcibly raises the question again of whether a bone homologous with the accessory palatine or dermopalatine of *Amia* is present in primitive characoids.

ECTOPTERYGOID TEETH. The presence of ectopterygoid teeth seems to have a mosaic distribution in characoids, and is sometimes a variable character. In the family Characidae, for example, ectopterygoid teeth are absent in *Salminus*, *Brycon*, and *Alestes* but are present in such highly specialized genera as *Acestro-rhynchus* (fig. 20) and *Serrasalmus*. In some characoids, such as *Boulengerella*, ectopterygoid teeth are minute or obsolescent. In characids with enlarged jaw teeth, the ectopterygoid dentition is generally absent or suppressed. Teeth are absent on the reduced ectopterygoid of *Pocilobrycon harrisoni*, but are present in some other members of the Nannostomina. Some specimens of *Pocilobrycon eques* were found in which teeth were absent on one ectopterygoid and present on the other (Weitzman, 1964, p. 144). This might be due to some sort of tooth replacement phenomenon.

Note. Ectopterygoid teeth in most characoids are simple conical teeth. *Serrasalmus*, however, has ectopterygoid teeth with the same peculiar morphology as the jaw teeth.

SYMPLECTIC BONE. In teleosts, in which both facets for reception of the bicipital articular surfaces of the lower jaw are generally formed on the quadrate bone, there has been a general evolutionary tendency for the symplectic bone to lose most of its connections with other bones, to become reduced in size, and finally to be lost.

In *Amia* the symplectic is fairly large with its dorsal edge firmly abutted against the ventral edge of the quadrate and its ventrolateral edge against the medial face of the lower preopercular limb. It is expanded posteriorly where it approaches the lowermost portion of the hyomandibular bone, and anteriorly it ends in a large socket which provides for one half of the bicipital articulation of the lower jaw. In the primitive teleost *Albula*, the symplectic is an expanded lamellar bone, extensively in contact with the hyomandibular and mesopterygoid bones as well as with the quadrate and preopercle, but its anterior end is pre-

vented from contacting the lower jaw by the anterior limb of the preopercle, which is in intimate contact with the quadrate. Both facets for articulation with the lower jaw are formed on the quadrate bone. In many teleosts, on the other hand, including the catfishes, the symplectics have been entirely lost. In characoids the symplectics are invariably present but are substantially reduced compared to those of *Albula* and *Amia*.

In all characoids the symplectic is a tubular bone of moderate dimension, its anterior portion fitting snugly into a groove in the medial face of the quadrate. The posterior end approximates and is synchondrally joined to the tubular, descending process of the hyomandibular bone, but scarcely or not at all contacts the mesopterygoid and the preopercle. Except for some variation in size, the condition of the symplectic bones seems to change relatively little from group to group of characoids.

FACIAL BONES

NASAL BONE. Sagemehl (1885, p. 32) pointed out that the nasal bone in Erythrinidae and *Hepsetus* is remarkably large for teleosts and compared it with the nasal of *Amia*. A large, lamellar nasal bone, firmly articulated to the skull and bearing a bony canal for investiture of the nasal portion of the cephalic lateral line, is also present in Ctenoluciidae.

In the majority of characoids, as in *Agoniates* (Géry, 1963a, figs. 3, 4, 6), *Acestrorhynchus*, and *Brycon*, the nasal bone is represented only by the bony canal enclosing the nasal portion of the cephalic lateral line canal, and is relatively loosely articulated to the skull. *Salminus* and *Alestes* are perhaps intermediate between those characoids having a large lamellar nasal bone and those in which the nasal bone is reduced to a mere bony canal. The nasal bone is lacking in *Lepidarchus adonis* (Roberts, 1966, p. 210).

CIRCUMORBITAL BONES. Probably characoids primitively had an orbital ring of eight bones: a supraorbital, an antorbital, and six infraorbitals, according to the terminology of Weitzman (1962, pp. 28-31). Eight is the highest number of orbital bones ordinarily found in characoids, and it is characteristic of such primitive or generalized characoids as *Hepsetus*, *Brycon*, and *Salminus*, and also occurs in some highly specialized genera.

Both the supraorbital and the antorbital (at least as a separate element) are lacking in *Hoplias*, which has all six infraorbitals. Another peculiarity of the circumorbital series of *Hoplias* is that one or more infraorbital elements are excluded from the rim of the orbit. In a 58.5-mm. specimen the proximal ends of the third and fifth infraorbitals meet in the orbital rim, thereby excluding the fourth infraorbital (fig. 3). Alexander (1965, fig. 9, p. 185) has figured a larger specimen in which the second and fifth infraorbitals meet proximally, thereby excluding both the third and fourth.

In *Ctenolucius* the antorbital is lacking and there are only five infraorbitals:

the third infraorbital is exceptionally large and may have been derived from fusion of the primitive third and fourth infraorbitals (fig. 2). In *Hepsetus*, unlike any other characoids, the supraorbital has a distinct ventral limb articulating directly with the first infraorbital; the antorbital is thereby excluded from the orbital rim. The posterior portion of the antorbital lies in a groove or shallow depression in the leading edge of the ventral limb of the supraorbital bone (fig. 1). In *Brycon* and *Salminus* (fig. 4) the antorbital bone forms part of the orbital rim.

Although the orbital bones have been reduced in many groups of characoids (and in gymnotoids they are usually represented only by bony tubes bordering the orbit which enclose the infraorbital branch of the cephalic lateral line), in primitive or generalized characoids they are exceptionally large, compared to those of teleosts as a whole. The third infraorbital, which is usually the largest, occupies much of the cheek region. In primitive or generalized characoids in which the dorsolateral edge of the skull is more or less straight (e.g., *Salminus*, *Hoplias*, *Hepsetus*, and *Ctenolucius*) the sixth infraorbital is large and has a more or less straight edge which is firmly articulated to the edge of the skull. Often in specialized characoids, for example *Acestrorhynchus*, the sixth infraorbital is greatly reduced and has relatively little articulation with the skull (fig. 5). In some instances it is little more than a segment of the bony canal enclosing the dorsalmost portion of the infraorbital branch of the cephalic lateral line.

Reduction of the circumorbital bones has occurred in many lines of characoids. In some instances, as in *Acestrorhynchus*, this is probably related to reduction of the sixth infraorbital and the resulting loss of an extensive, firm suspension for the dorsoposterior limb of the infraorbital series. The third infraorbital is truncated distally, so that it fails to extend downwards all the way to the preopercle. The circumorbital series of *Acestrorhynchus* is also specialized in that the posteroventral portion of the first infraorbital extends ventrally to the second infraorbital and acts as a sheath or scabbard for the heavily toothed posterior portion of the maxillary which extends beyond the gape.

Gosline (1965, p. 188) stated that in the amioids (most closely approached among teleosts by the erythrinid characoids), the dermosphenotic [= sixth infraorbital] forms one of the roofing bones of the skull, and the hinge line for the circumorbital series movement lies below it. This statement should be slightly amplified. If one lifts the opercle of a preserved specimen of *Amia*, the infraorbital series ventral to the sixth infraorbital is lifted with it, while the sixth infraorbital remains unchanged in position. In *Hepsetus* and *Salminus*, as well as in erythrinids, the major movement in the circumorbital series is still between the sixth and fifth infraorbitals. In these characoids there is also a slight lifting of the sixth infraorbital (this is most noticeable in *Salminus*) and the fifth infraorbital slips partially beneath or inside the sixth infraorbital, whereas in *Amia*

the adjacent edges of the fifth and sixth infraorbitals meet end on. In *Ctenolucius* the firm junction between the sixth infraorbital and the large infraorbital below it prevents any hinge-like movement, and the infraorbital series is not readily moved by lifting up the opercle. In characoids in which the sixth infraorbital is greatly reduced the entire infraorbital series is readily moved by lifting up the opercle.

OPERCULAR BONES. The opercular series is complete in all characoids; that is, preopercle, opercle, interopercle, and subopercle are always present.

A lamellar supraopercle is present among characoids only in Hepsetidae and Erythrinidae. In these two families the sixth infraorbital bone has an exceptionally extensive articulation with the lateral margin of the cranium, and posteriorly the sixth infraorbital approximates or contacts the anterior edge of the supraopercle. The absence of the supraopercle in other characoids may be related to the reduction of the sixth infraorbital. The supraopercle in Hepsetidae and Erythrinidae is not the same as the supraopercle which has been reported in some other characoids, e.g., in *Acestrocephalus anomalus* (Weitzman, 1962, p. 32). In *Acestrocephalus anomalus* and in many other characoids the dorsal portion of the bony canal enclosing the preopercular branch of the cephalic lateral line often extends considerably above the preopercle bone proper. Sometimes this dorsal portion forms separately and later fuses with the main body of the bony canal and the preopercle bone, but in some species it remains separate. Such an element is present in *Hepsetus* (labeled "autogenous preopercular canal bone" in fig. 1), and is clearly distinct from the lamellar supraopercle.

In *Hepsetus* the supraopercle bears a short segment of bony canal along its anterior margin for investiture of a portion of the preopercular branch of the cephalic lateral line. In *Hoplias* it does not. In *Acestrorhynchus* the dorsoposterior corner of the opercle extends dorsally as a peculiar flange (fig. 5).

SUBOPERCLE. In *Amia* the subopercle is firmly ankylosed to the opercle, as well as to the interopercle; it has a strong, dorsally directed process which is immovably joined to the anterior edge of the anteroventral corner of the opercle. In some of the lower teleosts and in percomorphs in general, the subopercle is similarly joined to the opercle by a dorsally directed process. In characoids, however, the subopercle is invariably loosely articulated only by connective tissue to the opercle and interopercle, and the dorsal process of the above-mentioned fishes, if present at all, is reduced to a minute flange (fig. 26, *Hepsetus*).

HYOID ARCH

BASIHyal. In most characoids the basihyal is more or less uniformly slender. In *Hoplias*, however, the basihyal is expanded anteriorly into a wide horizontal lamella with a broadly rounded margin (fig. 35). In *Hoplias* (as in Erythrinidae generally) the tongue is unusually broad and relatively free from the floor of the mouth compared to the tongue in most other characoids.

BRANCHIOSTEGAL RAYS. Most characoids—including *Hepsetus*, *Ctenolucius*, *Salminus*, and *Acestrorhynchus*—have four branchiostegal rays. *Poecilobrycon* has three (Weitzman, 1964), as does *Curimatus isognathus*. Some characoids have five, including Erythrinidae, *Piaractus nigripinnis*, *Agoniates* (according to Géry, 1963a, p. 272, *Agoniates* has five branchiostegal rays, of which the anterior two are rudimentary), *Hydrolycus*, *Rhaphiodon* (Nelson, 1949, p. 503, pl. 6, fig. 10), and the gasteropelecid *Thoracocharax* (Weitzman, 1960b, p. 233).

Weitzman (1960b, p. 233) was of the opinion, based on Hubbs (1919), that reduction in the number of branchiostegal rays is a general evolutionary trend in characoids. He cited the presence of five branchiostegal rays in *Thoracocharax* as part of the evidence that at least in certain respects it is the most primitive genus in the family Gasteropelecidae, the rest of the members of which have only four branchiostegal rays.

GILL ARCHES

GENERAL FEATURES. The branchial arches and associated gill rakers and teeth of *Amia*, which are more generalized than in any teleosts, may be remarked upon before considering these structures in characoids. *Amia* has five branchial arches, the first four of which are complete. The fifth arch consists of paired upper pharyngeals (or epibranchials), paired lower pharyngeals (or ceratobranchials), and a median basibranchial. The gill filaments are supported by gill rays. Gill rakers are present on the leading and on the trailing edges of the first four gill arches and on the leading edge of the fifth ceratobranchial or lower pharyngeal. Teeth are present in dense patches on the suspensory pharyngeals (including the anteriormost one), upper and lower pharyngeals, and fifth basibranchial (absent on other basibranchials). Irregular rows or patches of teeth extend between the gill rakers on the first four gill arches, and each gill raker is itself covered with a dense patch of teeth.

In teleosts, including characoids, there has been a marked tendency for branchial teeth, gill rakers on the trailing edges of the arches, and portions of the fifth branchial arch to be reduced or lost. The fifth basibranchial is usually absent in teleosts and is not found in any characoid. In many teleosts branchial teeth are present only on the upper and lower pharyngeals (fifth pharyngobranchials). Nevertheless, teeth have been retained on the gill rakers in numerous teleosts, including many characoids, and in many characoids teeth are also present on the second and third suspensory pharyngeals. In *Hoplias*, in addition to the normal complement of gill rakers, there are some thin, tooth-bearing osseous plates, which may or may not be gill rakers, on the proximal portions of the anterior gill arches and extending anteriorly along either side of the basihyal (fig. 35). The rows of gill rakers on the trailing edges of the gill arches are usually lacking in higher teleosts but are retained to some extent in many lower teleosts including characoids. In *Hoplias* they are present on all of the gill

arches. It may be noted that in characoids and in gymnotoids the gill rakers on the trailing edge of the branchial arches appear first during development on the fourth arch, next on the third arch, then the second arch, and often fail to develop on the first arch.

Bony gill rays supporting the gill filaments are lacking in the majority of characoids, but are present in *Acestrorhynchus* (fig. 37).

Note. Epibranchial organs have been reported in several highly specialized characoids (*Prochilodus*, *Curimatus*, *Caenotropus*, and *Citharinus*; Thys van den Audenaerde, 1961, p. 146) but the morphology of these structures has not been thoroughly investigated and they may be unrelated to the epibranchial organs found in other teleosts. A peculiar, sac-like epibranchial organ in the highly specialized African catfish *Synodontis membranaceus* is probably also of independent origin. Epibranchial organs are lacking in *Salminus*, *Ctenolucius*, *Hepsetus*, *Hoplias*, *Brycon*, and *Acestrorhynchus*.

GILL RAKERS. Apparently gill rakers primitively were flattened, tooth-bearing bony lamellae forming two series on the leading and trailing edge of the gill arches. Perhaps they were more or less morphologically identical on all of the arches, as are the evidently relatively primitive rakers of *Polypterus*, *Lepisosteus*, and *Esox*. In most fishes, however, the gill rakers are differentiated, those of at least the first arch usually being relatively prominent and sometimes specialized in other ways. In many teleosts the rakers on the trailing edge of the arches (if they have not been lost) and on the posteriormost arches are relatively primitive morphologically; this is generally the situation in characoids.

Among characoids, perhaps the condition of the gill rakers is relatively primitive in such genera as *Hoplias*, *Acestrorhynchus*, and *Rhaphiodon*, in which the gill rakers are present on both the leading and trailing edges of all the arches, are all tooth-bearing, and exhibit relatively little differentiation on successive arches. In *Hoplias* a few rakers on the ceratobranchial of the first arch are much more elongate than the rest of the rakers (fig. 35). In *Rhaphiodon* and *Acestrorhynchus* (fig. 37) the gill rakers on all of the arches are thin lamellae closely adherent to the gill bars. The teeth are slightly larger and somewhat fewer on the more anterior arches. It is possible that the gill rakers have become secondarily reduced in some characoids. In *Salminus* the first two gill arches lack rakers on their trailing edges, whereas most of the rakers on the leading edge are enlarged. In *Hepsetus* and *Ctenolucius* (figs. 33, 34) some of the anterior rakers are elongate and toothless; the absence of teeth is probably a specialized condition. The posterior rakers appear to be morphologically relatively primitive.

Preliminary observations of young stages of *Hydrocynus* and *Gymnotus* indicate that the posterior gill arches develop gill rakers on their trailing edges before the anterior arches. I suspect that in many characoids the anteriormost

arch is the last arch to develop gill rakers on its trailing edge. If this is so, then it is not surprising that some characoids fail to develop rakers on the trailing edge of the first arch even when the remaining arches are well provided with them. Further observations should be made on the sequence of gill raker development.

PHARYNGEAL TEETH. In practically all characoids the pharyngeal dentition consists of simple conical teeth. They may be very numerous and generally cover a major portion of the pharyngeal bones.

The only characoids with complex pharyngeal dentition that I know belong to the families Chilodontidae and Anostomidae, which characteristically have peculiar multicuspid pharyngeal teeth with hollow stalk-like bases and two or three recurved cusps which are graduated in size. As in the multicuspid characoid jaw teeth, there is a distinct zone between the cusps and the base which transmits light more readily, and the cusps represent separately formed conical elements (verified in an alizarin preparation of *Chilodus*). Before I compared the pharyngeal teeth of *Chilodus* with those of *Leporinus*, *Rhytioidus*, and other Anostomidae, Weitzman had mentioned in discussion the possibility that the Chilodontidae and Anostomidae are closely related. I expect further study to show that the Chilodontidae represent a specialized subfamily of Anostomidae. Géry (1964) reviewed the species of Chilodontinae and figured the pharyngeal teeth of *Caenotopus maculosus* and *Chilodus punctatus*.

Note. The multicuspid pharyngeal and primary jaw teeth in some species of *Tilapia* (see Poll, 1957, figs. 321, 323)—an African genus of the percomorph family Cichlidae—are extremely similar to those of some of the Anostomidae. This amazing convergence of trophic structures occurs in fishes which are entirely different in body form and swimming movements. In the Anostomidae, as in other characoids, replacement teeth arise in back of the functional tooth rows. In *Tilapia*, as in *Girella* (Norris and Prescott, 1959) and in some of the browsing catfishes of the genus *Synodontis*, the replacement teeth come up in front of the functional teeth.

WEBERIAN APPARATUS

In characoids the four centra of the Weberian apparatus are normally separate. Weitzman (1962, p. 36) reported a specimen of *Carnegiella vesca* in which the third and fourth centra were abnormally fused. The Weberian apparatus was otherwise normal. My figure of the Weberian apparatus in *Lepidarchus* (Roberts, 1966, fig. 6) gives the impression that the first and second centra are fused, whereas they actually are separate.

The first centrum is a simple disc with dorsolateral depressions to receive the ventral articular process of each scaphium. In cyprinoids the first centrum usually bears a short but stout lateral process. This process is never present in characoids.

The second centrum bears a lateral process and usually dorsolateral or lateral depressions to receive the ventral articular process of each intercalarium. In *Hepsetus* the intercalarium has a well developed acetabulum which fits into a dorsolateral excavation in the second centrum (fig. 38). The main body of the intercalarium is a curved shaft. The anteroventral end is notched in some characoids. In *Ctenolucius* the dorsoposterior end is deeply forked (fig. 40), but in other characoids it is simple. In *Hepsetus* the second centrum has a pair of posteriorly projecting processes which arise on the anterior portion of its ventral surface (fig. 39). These processes extend posteriorly until they almost contact a pair of relatively short, anteriorly projecting processes from the ossa suspensoria of the fourth centrum. There are no projections or processes on the ventral surface of the second centrum in *Ctenolucius*, *Hoplias*, *Salminus*, or *Acestrorhynchus*.

The third centrum of *Hepsetus* differs from that of other characoids in having paired anterolaterally and posterolaterally projecting processes from its ventral surface (fig. 39). The tripus is somewhat variable in characoids. Many genera are apparently characterized by subtle differences in the form of the tripus. In *Hepsetus* the body and blade portions of the tripus are apparently connected to each other by cartilage alone. In other characoids they are united to a greater or lesser extent by co-ossification and tend to form a single bone. The blade portions of the tripus are ligamentously attached to the intercalarium, which is in turn ligamentously attached to the bowl, or "conch," of the scaphium.

The family Characidae is apparently typified by a dorsoanteriorly directed process from the neural arch pedicle of the third vertebra which is tightly bound into a groove-like fossa in the base of the neural complex. This process is present in *Piaractus*, *Serrasalmus*, *Hydrocynus*, *Salminus* (fig. 44), *Acestrorhynchus* (fig. 46), *Brycon* (Weitzman, 1962, fig. 12) and *Alestes* (Monod, 1950, figs. 100-101). Of the genera listed, its development is weakest in *Alestes*. There is no indication whatever of such a process in *Hepsetus*, *Hoplias*, *Distichodus*, *Pocilobrycon* (Weitzman, 1964, fig. 9), or *Carnegiella* (Weitzman, 1954, fig. 10). In *Ctenolucius* the neural arch pedicle has a minute dorsal projection (fig. 40) which is conceivably related to the process in Characidae.

In the characid genera *Brycon*, *Acestrorhynchus*, *Alestes*, *Piaractus*, and *Serrasalmus* the base of the neural complex extends posteriorly until it nearly touches the neural spine of the fourth vertebra. In *Hepsetus*, *Hoplias*, and *Ctenolucius* the base of the neural complex extends posteriorly only as far as the leading edge of the neural arch pedicle of the fourth vertebra, and the area between it and the neural spine is partially occupied by a supraneural bone (fig. 40 of *Ctenolucius*). The relation of the neural complex to the fourth neural spine in *Salminus* (fig. 44) is intermediate between the condition found in *Hepsetus*, *Ctenolucius*, and *Hoplias*, and that in the Characidae just listed.

The rib of the fifth vertebra bears near its base a medially directed process which is ligamentously attached to the os suspensorium of the fourth vertebra in *Acestrorhynchus* (figs. 46, 47), *Alestes*, *Piaractus*, and *Brycon meeki* (Weitzman, personal communication). This process is lacking in *Salminus*, *Hepsetus*, *Hoplias*, and *Ctenolucius*.

PECTORAL FIN

The generalized characoid pectoral girdle consists of an extrascapular; a posttemporal with an ascending limb joined by extensive fascia to the cranium and a descending limb connected by a strong ligament to the intercalar bone; a supracleithrum; a cleithrum; three postcleithra, of which the third is a slender strut-like bone; a mesocoracoid; a scapular; and a coracoid. Coracoid and cleithrum usually meet anteriorly and sometimes have interdigitating processes, but the latter are never as well developed or as firmly interdigitated as in catfishes. The cleithrum is attached to the occipital centrum by a strong ligament. This ligament, usually ossified in catfishes, is never ossified in characoids. The scapular foramen is usually very large. The first pectoral ray articulates directly with the scapula; the remaining rays articulate with radials, of which there are four in a proximal series and usually several smaller ones in a distal series.

It may be noted that in many characoids the young have a peculiar pedunculated pectoral fin which resembles the lobed pectoral fin in the young of *Amia*. In these characoids the pectoral fins are the last of the fins to develop rays, and the rays are formed in the peduncle; the dorsalmost rays develop first.

The following modifications of the pectoral girdle and fin sometimes occur in characoids: (1) loss of the extrascapular, (2) loss of the descending limb of the posttemporal bone. According to Sagemehl (1885), this is correlated with reduction of the intercalar bone. I reported that the descending limb is lacking in *Lepidarchus adonis* (Roberts, 1966, p. 213). I have re-examined specimens of *Lepidarchus* and reaffirm that the descending limb is missing. The ligament which usually attaches the descending limb to the intercalar bone is absent, as apparently is the intercalar bone itself. Regan (1911) stated that the descending posttemporal limb and intercalar bone are lacking in gymnotoids; (3) reduction of the number of postcleithra. Three postcleithra are found in many generalized characoids, including *Salminus*, *Brycon*, and *Hoplias*; some characoids have two postcleithra; *Hepsetus* and *Ctenolucius* have a single postcleithrum; (4) great expansion of cleithra and coracoids, in Gasteropelecidae, *Triportheus*, *Agoniates*, *Clupeacharax*, and Cynodontidae; (5) loss or fusion of radials; distal radials are absent in many species. In *Carnegiella vesca* there are only three proximal radials and in *C. myersi* the proximal radials have fused into a single element (Weitzman, 1954, p. 225); (6) in Gasteropelecidae the posttemporal and supracleithrum apparently are fused into a single bone (Weitzman, 1960,

p. 217); (7) the lowermost pectoral rays in *Hepsetus* and *Ctenolucius* are unlike those found in the adults of other characoids. In these two genera the ray halves of the lowermost rays do not fuse but remain separate and fail to articulate directly with radial bones; the condition of these rays is evidently related to the relatively late retention in both genera of the pedunculated condition of the pectoral fin found in the young of many characoids; (8) reduction of the coracoid bone in Erythrinidae (noted by Weitzman, 1964, pp. 135, 148, 151). The pectoral girdle and coracoid bone of half-grown *Hoplias* (fig. 51) is very similar to that of a young, 42 mm. *Hepsetus odoc* (fig. 49). Judging from this observation, the pectoral girdle of *Hoplias* may be neotenic. It should be noted that distal radials have failed to develop in the pectoral girdle of the half-grown individuals of *Hoplias*, whereas they are present in half-grown specimens of *Hepsetus*; (9) in characoids with specialized pectoral girdles the left and right coracoid bones are often adpressed to each other medially for their entire lengths, whereas in characoids with more or less generalized pectoral girdles, including *Hepsetus*, *Hoplias*, *Ctenolucius*, and *Salminus*, the coracoids are in contact only anteriorly.

Most characoids have four proximal radials. The median or uppermost of the radials is usually trilobate distally, its appearance suggesting that either three distal radials have fused with an originally simple median proximal radial or else that the median proximal radial represents three fused proximal radials. In *Brycon* the median proximal radial is trilobate, and each of the lobes articulates with a small distal radial (Weitzman, 1962, p. 41; fig. 20, p. 76).

PELVIC FIN

The pelvic bone and ischiac process are readily distinguishable in the pelvic girdle of practically all characoids.

The number of pelvic fin rays ranges from five (in Gasteropelecidae) to 11 or 12 (Distichodontidae, Citharinidae, *Hemiodus*). Most members of the family Characidae, including *Brycon* and *Salminus*, have eight. *Ctenolucius* has eight and *Hepsetus* has nine.

Pelvic splints lateral to the outermost pelvic rays are apparently present in all characoids (for a discussion of pelvic splints in fishes generally, see Gosline, 1961).

Weitzman (1962, p. 42) reported three radial bones between the pelvic fin ray halves in *Brycon meeki*. Three similarly situated ossified radials are present in *Hoplias* and in *Salminus* (presence or absence not verified in other characoids).

CAUDAL FIN

HYPURALS. All characoids have a caudal skeleton with the basic number of seven hypurals. Reductions of this number are probably all due to fusion. Seven

separate hypurals are invariably present in very small specimens. Fusion between the fifth and sixth hypurals is apparently rather common in characoids, and the third and fourth are occasionally fused, as in the 94 mm. specimen of *Hepsetus* represented in figure 56. Specimens of *Hepsetus* 19, 22.5, and 58.5 mm. in standard length have seven separate hypurals.

The hypurals remain separate in some very large specimens of characoids. There are seven hypurals in a 528 mm. specimen of *Piaractus nigripinnis*, and there appear to be seven separate hypurals in radiographs of a 290 mm. example of *Hepsetus* and a 355 mm. one of *Ctenolucius*.

URONEURALS. Weitzman (1962, p. 39, fig. 15, p. 71) found two pairs of uroneurals in *Brycon meeki*. I have detected what appear to be two separate pairs of uroneurals in radiographs of large specimens of *Hepsetus* and of *Ctenolucius*. On the other hand, careful dissection of caudal skeletons of *Hoplias* of several different sizes revealed only a single pair of uroneurals. Fuster de Plaza (1950, fig. 18, p. 199) showed two uroneurals in the caudal skeleton of *Salminus*, but her uroneural I is actually the urostyle. My dissection reveals two pairs of uroneurals in *Salminus*, the distal pair of which is very small, lies ventral to the very large proximal pair and medial to the proximal portions of the ray halves of one of the uppermost principal caudal fin rays. In *Salminus* there is an osseous element passing from the distal end of the posterior epural across the distal ends of the urostyle and proximal uroneural and ending near the ventral surface of the proximal portion of the ray halves of one of the posteriormost procurrent caudal rays. This element is not a uroneural; it appears, rather, to be an ossified ligament.

EPURALS. The number of epurals varies in characoids from one to three. Three occur in *Hepsetus*, *Ctenolucius*, *Brycon*, *Hydrocynus*, *Lepidarchus*, and in Anostomidae (observed in *Anostomus*, *Leporinus*, and *Schizodon*). Two occur in *Salminus*, *Serrasalmus*, *Piaractus*, *Poecilobrycon*, and the African family Distichodontidae (verified in *Distichodus fasciolatus*, *Congocharax olbrechtsii*, and *Xenocharax spilurus*). A few characoids, including *Agoniates* (Géry, 1963a) and *Hoplias*, have but one epural.

Apparently the caudal skeleton of characoids primitively had three epurals, and there has been an evolutionary trend for reduction of this number. It is noteworthy that in all characoids with three epurals the bases of several of the procurrent caudal rays are articulated with the distal ends of the epurals. In *Agoniates* and *Hoplias*, in contrast, the single epural element is very slender and in *Hoplias* only one procurrent ray articulates with it (fig. 58) (the relations of the epural in *Agoniates* to the procurrent rays is unknown, but it appears unlikely that more than one procurrent ray articulates with it).

PROCURRENT CAUDAL RAYS AND ASSOCIATED STRUCTURES. Perhaps the most generalized condition of the procurrent rays in characoids is that in which they

are moderately numerous and the numbers in the upper and lower series are about equal, as in *Hepsetus* and *Salminus* (figs. 56, 59). Evolutionary trends involving the procurrent rays are apparently (1) a general tendency for reduction in their number, and (2) loss of articulation with the epurals, sometimes with the development of new structures for articulation or support. In *Hepsetus* and *Salminus* many of the upper procurrent rays articulate directly with the epurals, and the rest with the distal ends of neural spines.

The 52.5 mm. specimen of *Hoplias* represented in figure 58 has eight upper but only four lower procurrent rays. The anteriormost four upper rays articulate with a slender bony stay, the next three articulate with neural spines, and the last one articulates directly with the single slender epural.

In *Ctenolucius* there are four upper and four lower procurrent rays. The upper ones have still largely retained their articulation with the epurals. Immediately anterior to them, however, is a large, vertical plate-like bone. A similar bone is associated with the lower procurrent rays. These bones (labeled "bony stay" in fig. 57) are apparently dermal elements, for no cartilage is detectable at their edges, and it seems likely that they originated from fusion of anterior procurrent rays. An analogous pair of structures, although much smaller, are associated with the procurrent rays in the caudal skeleton of *Hydrocynus* (fig. 60).

Eigenmann (1915) pointed out that in many of the American characids of the subfamily Cheirodontinae the lower procurrent caudal rays [= interhaemals of Eigenmann] are peculiarly modified. In certain instances the lower procurrent rays are more numerous than in any of the primitive or generalized characoids. An extreme example is *Cheirodon interruptus*, which has 17 to 27 procurrent rays extending from the caudal fin to the anal fin (Eigenmann, 1915, pp. 72, 73, fig. 24). It is evident that in some sections of the Cheirodontinae there has been an evolutionary tendency to increase the number of lower procurrent caudal rays.

CHARACTERISTICS OF THE PRIMITIVE AFRICAN FAMILY HEPSETIDAE

Habitus pike-like; body elongate, subcylindrical; jaws elongate, with numerous sharp conical teeth; nine-rayed dorsal and 11-rayed anal fins set far back on body, dorsal fin entirely posterior to pelvic fins; adipose fin small, its base above last two or three rays of anal fin; caudal fin deeply forked; scales cycloid, about 50 to 60 in a longitudinal series; lateral line complete; air bladder normal, not cellular, posterior chamber longer than anterior chamber but not prolonged beyond body cavity, both chambers simple; membranous flap projects from either side of the upper jaws and a larger membranous flap projects from either side of the lower jaws (similar flaps project from the lower jaws of *Cteno-*

lucius but are absent from the upper jaws); olfactory bulbs lie immediately anterior to lobes of forebrain, and olfactory nerve passes directly through the anterior portion of the orbit on its way to the nasal organ.

Teeth conical through life; lower jaw with an outer row of large, sharp teeth of variable size, and an inner row of small teeth of uniform size lying internal to a shallow replacement trench for the outer row; toothed portion of maxillary extending beyond gape; replacement teeth lie in gum immediately at bases of functional teeth.

Skull with many primitive or generalized features: cranial roof flattened and highly sculptured; supraoccipital crest low; insertion of dorsoanterior scale rows continuous with posterior margin of parietal bones; cranial fontanel completely closed in adults; occipital region of skull moderately sloping (not as sloped as in Erythrinidae and Lebiasinidae, but definitely more sloped than in most characoids); lateral margin of cranial roof straight; nasal bone lamellar; circumorbital series complete, infraorbitals large, lamellar; sphenotic spine strong, extending well beyond lateral margin of skull roof; dilator groove entirely posterior to sphenotic spine, not extending onto skull roof; sixth infra-orbital with extensive frontoparietal articulation; posterior portion of antorbital lying in a shallow depression in the supraorbital bone and excluded from the rim of the orbit; orbit relatively small; lamellar canal-bearing supraopercular bone present (lamellar supraopercle also present in Erythrinidae but lacking a canal); separately ossifying portion of canal enclosing preopercular branch of cephalic lateral line present dorsal to preopercle; extrascapular present; palate with a tooth-bearing bone lying between the ectopterygoid and maxillary bones, possibly homologous with the accessory palatine or dermopalatine of Erythrinidae and *Amia*; ectopterygoid toothless; metapterygoid-quadrangle foramen present; posttemporal fossae with moderately large dorsal oblique and ventrolateral vertical openings of an apparently generalized nature for characoids; premaxillaries immovably articulated to ethmoid bone; ethmoid spine projecting between premaxillaries; maxillaries movably articulated to cranium and to premaxillaries; parasphenoid straight; orbitosphenoid sutured to parasphenoid; rhinosphenoid absent; posterior portion of maxillary almost entirely covered by first and second circumorbital bones when the mouth is closed; branchiostegal rays four; gill openings broad, gill membranes free from each other and free from isthmus.

Pectoral girdle, Weberian apparatus, caudal skeleton, hyoid, and branchial arches generalized; second centrum with a pair of posteriorly projecting processes arising from its ventral surface; tripus with distinct body and blade portions which are not fused together but joined by an apparently cartilaginous tissue; pectoral girdle with a single postcleithrum; young with lobed or pedunculated pectoral fins; fifth ribs without medially directed processes; upper and lower procurrent rays equal in number, moderately numerous, upper rays articulating

mainly with epurals, of which there are three; vertebrae 44 or 45 (28 + 16, Boulenger, 1909, p. 177; 30 + 15 in two specimens from Ghana).

This family is represented by a single species, *Hepsetus odoe* (Bloch), which is widely distributed in tropical Africa but excluding the Nile basin.

CHARACTERISTICS OF THE AMERICAN FAMILY CTENOLUCIIDAE

Habitus pikelike; body very elongate, subcylindrical; jaws extremely elongate, with numerous small recurved conical teeth; dorsal and anal fins short based and set further back on the body than in any other characoids excepting those in the family Cynodontidae; adipose fin small, its base above last two or three rays of anal fin; caudal fin deeply forked; scales strongly ctenoid or very weakly ctenoid; lateral line complete; air bladder normal, not cellular, posterior chamber longer than anterior chamber but not prolonged beyond body cavity, both chambers simple.

Teeth conical throughout life. The exact form of the teeth is peculiar. In *Boulengerella* all of the teeth and in *Ctenolucius* most of the teeth have recurved crowns (Roberts, 1967a, fig. 1) unlike the teeth in any other characoids. In *Ctenolucius* some of the anteriormost premaxillary and dentary teeth have a more normal conical form. An internal row of conical teeth in the posterior portion of the lower jaw inside the replacement trench for the external tooth row may be present (*Ctenolucius*) or absent (*Boulengerella*). Replacement teeth lie in the gum immediately at the bases of the functional teeth. Ectopterygoid with numerous fine conical teeth.

Cranial roof flattened, highly sculptured, cranial fontanels closed in adults; occipital slope moderate, as in *Hepsetus*; lateral margin of cranial roof straight; nasal bone lamellar; circumorbital bones reduced in number to six; antorbital missing as a separate bone; third and fourth circumorbitals apparently fused into a single large element; sixth infraorbital with an extensive frontal articulation; fifth infraorbital with extensive pterotic articulation; extrascapular present; supraopercle absent; dermopalatine or accessory ectopterygoid absent; ectopterygoid with numerous small conical teeth; metapterygoid—quadrate foramen present; posttemporal fossae with moderately large dorsal oblique and ventrolateral vertical openings; premaxillaries extremely elongate, immovably articulated to ethmoid bone; maxillaries fused to premaxillaries and largely excluded from the gape of the mouth; maxillaries largely covered by first and second circumorbital bones; parasphenoid bone straight; orbitosphenoid sutured to parasphenoid; rhinosphenoid absent; caudal skeleton with three epurals; upper and lower procurrent rays greatly reduced in number, the anteriormost ones apparently having fused to form large median bony stays. Pectoral girdle, Weberian apparatus, hyoid, and branchial arches generalized; pectoral girdle with a single postcleithrum; young with lobed or pedunculated pectoral fins; fifth ribs without medially directed processes; gill openings broad, gill mem-

branes free from each other and free from isthmus; branchiostegal rays four; vertebrae 42-48.

This family is represented by two genera, *Ctenolucius* and *Boulengerella*, with a number of species widely distributed in the tropics of Central and South America.

DISCUSSION

COMMENTS

The primary freshwater fishes of the ostariophysan suborder Characoidei are among the dominant elements in the rich ichthyofaunas of South America and Africa. They apparently have been confined to these two continents until relatively recently in geologic time, and probably were present in the Mesozoic before the episode of Continental Drift which separated Africa and South America. Subsequently there have been adaptive radiations of characoids on both continents, and they are probably far more numerous today than when the continents separated. Their phylogenetic history undoubtedly covers a very long period of time and the relationships of various groups are obscure. Convergent evolution is evident at all taxonomic levels, and many characters have a discontinuous or mosaic distribution.

Should they become available, well preserved characoid fossils from Mesozoic or early Cenozoic deposits would be extremely interesting. Fragmentary fossils or ones on which detailed osteological studies are impossible will probably not be very helpful. Inadequate morphological information about the living characoids has been as much of a handicap to students of their phylogeny as the paucity of fossil material. Osteological information is practically the only kind of information that we are likely to get from fossil characoids, and this would be relatively useless without a sound knowledge of the osteology of living forms.

We do not know how many distinctive types of characoids have become extinct. I suspect that most of the major phyletic lines have extant representatives, and that a reasonably satisfactory picture of phylogenetic trends within the Characoidei can be worked out from the living forms, which include many primitive and annectant genera. In Africa, for example, the genus *Xenocharax* is morphologically generalized and appears to be basal to the peculiar endemic families Citharinidae, Ichthyboridae, and Distichodontidae. The citharinid *Citharidium* appears to be annectant between *Xenocharax* and the peculiar genus *Citharinus*, while *Paraphago* is probably annectant between *Xenocharax* and some of the most peculiar ichthyborid genera. With a reasonable amount of morphological study, a fairly complete family tree of these African families could perhaps be worked out. The only other characoids in Africa are *Hepsetus*, discussed below, and members of the Characidae, a family which is also represented in South America. In South America numerous genera may be annectant

between groups, and classification of the American characoids is not liable to be materially improved as long as such genera remain to be morphologically investigated.

In this study attention has been directed to the osteology of *Hepsetus*, *Ctenolucius*, *Hoplias*, *Salminus*, and *Acetrorhynchus*. It was felt *a priori*, as explained in the Introduction, that these particular genera would provide insights into broad problems of characoid phylogeny. We shall now consider various topics stemming more or less directly from the osteological study of these genera. There is a list of the main conclusions reached in this paper at the end of the Discussion.

RELATIONSHIP OF HEPSETIDAE AND CTENOLUCIIDAE

As previously pointed out (Roberts, 1966, p. 215), many features of *Hepsetus* are not found in the African Characidae, a relatively homogeneous group in which the majority of species have multicuspid teeth and belong to a few clearly related genera. The remaining African characoids belong to highly peculiar families, the relationships of which are uncertain, but they are evidently not closely related to *Hepsetus*, which is far more generalized. Of all characoids, the American genera *Ctenolucius* and *Boulengerella* bear the closest resemblance to *Hepsetus*. They share with it such general characteristics as elongated jaws and subcylindrical body, conical dentition, short dorsal and anal fins placed further posteriorly than in any other characoids, a flattened, highly sculptured cranial roof without fontanels, a low supraoccipital crest, and large circumorbital bones. The oral flaps, shallow replacement tooth trenches, and peculiar pectoral fin rays are also suggestive of relationship.

Yet differences between *Hepsetus* and *Ctenolucius* and *Boulengerella* are such as fully to warrant placing them in separate families. *Hepsetus* has the following bones which are absent in *Ctenolucius* and *Boulengerella*: a large, tooth-bearing palatal element (absent in other characoids with possible exception of Erythrinidae); an antorbital; and a canal-bearing, lamellar supraopercle (as well as a small autogenous preopercular canal bone). *Ctenolucius* and *Boulengerella*, on the other hand, have a pair of large median dermal bones in the anterior portion of the caudal skeleton which are lacking in *Hepsetus*. In *Hepsetus* the primitive row of conical teeth internal to the mandibular replacement trench is complete, whereas it is restricted to the posterior third of the dentary in *Ctenolucius* and is lacking in *Boulengerella*. *Ctenolucius* and *Boulengerella* have peculiarly modified lateral ethmoids, and apparently the third and fourth infraorbital bones, separate in *Hepsetus*, have fused in *Ctenolucius* and *Boulengerella*. *Ctenolucius* and *Boulengerella* differ markedly from *Hepsetus* in the form of the sphenotic spine and of the dilator groove. *Hepsetus* has nine-rayed, and *Boulengerella* and *Ctenolucius* have eight-rayed pelvic fins. Finally, in *Ctenolucius* and *Boulengerella* the premaxillary is extremely elon-

gate, and the maxillary, which is immovably fixed to the premaxillary, is almost completely excluded from the gape. In *Hepsetus* the jaws are relatively generalized.

We may recognize the Hepsetidae and Ctenoluciidae as distinct families which may be related to each other; they do share some primitive features. Some of their general characteristics, however, are such as might have resulted from convergent evolution to a predaceous, pike-like habitus. *Hepsetus* is evidently not closely related to any African characoids, and *Ctenolucius* and *Boulengerella* do not appear to be more closely related to any American characoids than to *Hepsetus*. They are certainly not close to *Acestrorhynchus*. In many respects *Hepsetus* appears to be a very primitive characoid.

Hepsetus and *Ctenolucius*, as previously noted (Roberts, 1966, p. 216), have strikingly similar, fleshy, fimbriated flaps projecting from the sides of their jaws. Perhaps these structures are indicative of relationships, but it is possible that they arose independently. A peculiar modification of the oral membrane associated with the external row of teeth in the lower jaw has arisen independently in *Brycon labiatus* (Steindachner, 1880, pl. 3).

COMPARISON OF *BOULENGERELLA* AND *CTENOLUCIUS*

The present study has provided an opportunity to elucidate some of the differences between the two closely related genera of the family Ctenoluciidae. *Ctenolucius* was originally distinguished from *Boulengerella* by Gill (1861) on the basis of its ctenoid scales. As intimated by Gill (1895a), the ctenii of *Ctenolucius* are unlike ctenii found in other groups of characoids. In *C. hujeta* of 75 to 150 mm. in standard length, each scale has a dozen or so ridges or striae on its exposed shield which continue beyond the distal margin of the shield as ctenii. Ridges on adjacent scales are more or less aligned, providing an overall effect of numerous unbroken longitudinal ridges on the body. In 300 to 400 mm. specimens, the ctenii, although more numerous, are notably weaker, and the parallel pattern of the ridges is disrupted. Ctenii are present in *Boulengerella*, but are always numerous and very small, and the exposed sector of the scales bears irregular sculpturing rather than regularly arranged striae.

Ctenolucius and *Boulengerella* are morphologically and osteologically rather similar; the difference in their scales, in itself, would probably be insufficient to justify recognizing them as separate genera. There are, however, additional differences. The skull of *Boulengerella*, particularly the ethmoid region and the jaws, is more elongate than in *Ctenolucius*. The elongation of the upper jaw in *Boulengerella* involves lengthening of the premaxillary and a relative shortening of the maxillary. The fleshy, fimbriated flaps projecting from either side of the lower jaw in *Ctenolucius* are lacking in *Boulengerella*. In *Boulengerella* the teeth are all about equal in size and are arranged in single uniserial rows in both jaws; in *Ctenolucius* the teeth on the slightly expanded anterior region of the

premaxillary are enlarged, and in the lower jaw there is a short row of teeth lying internally to the mandibular replacement trench in addition to the external series of teeth. In *Ctenolucius* the ectopterygoid is provided with small conical teeth; in *Boulengerella* the ventral surface of the ectopterygoid is finely granulated, and anteriorly there are some very tiny conical teeth. The condition of these teeth in *Boulengerella* is perhaps related to the absence of the internal row of teeth inside the mandibular replacement trench, in which instance they may be considered obsolescent.

RELATIONSHIPS OF *SALMINUS*

Because of the very similar general appearance of *Brycon* and *Salminus*, one's first impression is that *Brycon* is *Salminus* with multicuspid teeth. Indeed, a general similarity between the two genera is apparent even in their osteology. I feel, however, that the osteological features common to *Brycon* and *Salminus* are shared because *Brycon*, despite its specialized dentition, is a fairly generalized characid, while *Salminus* is a primitive and relatively unspecialized characid. Osteological differences between the two genera are sufficiently numerous and their nature is such that direct derivation of *Brycon* from *Salminus* seems unlikely. In most of the ways that *Salminus* differs from *Brycon* it can be construed that *Salminus* is more primitive.

In *Salminus* all of the teeth are conical; the premaxillary and dentary have two rows of teeth and the maxillary has a single row. Excepting the anteriormost two premaxillary teeth in the internal row, which are as large as those in the external row, the teeth of the internal rows of the premaxillary and dentary are smaller and more numerous than those in the external rows. The external tooth row in the dentary is separated from the internal row by a shallow replacement trench. The replacement teeth for the external premaxillary row lie within the premaxillary bone, and those for the internal tooth rows of the premaxillary and dentary and for the maxillary tooth row lie in the gum at the base of each functional tooth (as in most Characidae, including *Brycon*). In adult *Brycon* all of the premaxillary and maxillary teeth and most of the dentary teeth are usually multicuspid. The maxillary teeth are all tricuspid; in *B. meeki* and *B. oligolepis* the premaxillary teeth are tricuspid except for the medial tooth in the innermost row, which is bicuspid, and the tooth beside it, which has four cusps. In the dentary, the large anterior teeth in the external row have either five or three cusps. Posteriorly the external row has a short series of conical teeth; although in *B. meeki* and *B. oligolepis* this series commences just behind the last multicuspid tooth in the external row, it lies medially to the external row and probably represents the internal row of conical teeth that formed part of the primitive characid dentition. In *B. falcatus* (the type species of *Brycon*) and *B. schomburgkii*, in fact, this row actually begins much further anteriorly, and is clearly medial to the external row. Immediately internal to the anteriormost

tooth of the external row, near the symphysis of the jaws, is an enlarged conical tooth. A pair of enlarged teeth in this position (one tooth on each side of the jaws) is characteristic not only of *Brycon*, but of the majority of the American and African Characidae with multicuspid teeth. In *Salminus* the teeth in the corresponding position are either small or absent. In the ways in which the dentition of *Salminus* differs from that of *Brycon*, the more primitive condition is probably represented in *Salminus*.

Note. Regan (1911, p. 18) stated that most of the teeth in *Salminus* are not truly conical, but approximate to the compressed and tricuspid type, especially in young specimens. Fuster de Plaza (1950, p. 172) stated that Salmininae have "dientes conicos o triangulares." In adult and half-grown specimens of *Salminus* the cutting edge of the tooth is posterolaterally flared basally, giving the teeth a somewhat triangular form, but the teeth are basically conical, i.e., they are not formed by the union of two or more separately formed conical elements. Conceivably the teeth of *Salminus* originated from multicuspid teeth, and it may be possible to demonstrate this in specimens smaller than those I have examined. This point is crucial to understanding the relationships of *Salminus*. If the apparently conical teeth of *Salminus* have been derived from multicuspid teeth (which I think is unlikely), then my ideas concerning the relationships of *Salminus* will have to be revised.

The lower jaw is relatively stouter in *Brycon* than in *Salminus*, correlated with its relatively massive dentition. The shape of the maxillary in *Brycon*, although unusual for characoids as a whole, is similar to that in many American Characidae including *Hemigrammus*, *Moenkhausia*, *Astyanax*. That is, the distal tooth-bearing portion of the maxillary is of about the same width for its entire length and its ventral edge is either straight or slightly convex. In *Salminus*, as in some other primitive characoids with well-toothed maxillaries, the tooth-bearing portion of the maxillary curves downwards, and thus its ventral edge is concave. The relatively light construction of the lower jaw and the shape of the maxillary in *Salminus* are probably primitive compared to the stout lower jaw and peculiarly-shaped maxillary of *Brycon*.

In *Salminus* each gill arch has a graded series of gill raker structures, with simple lamellar rakers at the hyal and cranial ends of the arch and modified rakers towards the angle of the arch. The appearance of these modified rakers clearly indicates their derivation from structures similar to the rakers at the ends of the arches. As in *Hoplias*, modification of the gill rakers has not proceeded very far; none of the rakers on the last three arches can be considered highly modified. In *Brycon* all of the rakers are relatively highly modified. The rakers on both the leading and trailing edges of each arch are relatively elongate at the cranial and hyal ends of the arch as well as towards its middle. In my opinion the gill rakers of *Salminus* are relatively primitive for characoids as a

whole, whereas those of *Brycon* are moderately specialized. The general trend for the gill rakers to become relatively prominent and elongate has had a much stronger effect in *Brycon* than in *Salminus*.

The infraorbital bones are considerably more expanded in *Salminus* than in *Brycon*. The orbit is relatively huge in *Brycon* (Weitzman, 1962, fig. 8, p. 64). The second infraorbital is more elongate in *Salminus*, evidently in connection with its role of serving as a sheath for the distal end of the maxillary bone when the mouth is closed. The sixth infraorbital is larger and its canal-bearing portion has a ventrally-projecting flange onto the dorsoanterior corner of the fifth infraorbital, which is absent in *Brycon*. A somewhat similar flange is present in *Ctenolucius*.

In general, the crania of *Salminus* and *Brycon* bear considerable resemblance to each other. It may be noted that in *Salminus*, unlike *Brycon*, the dilator groove is not continued onto the dorsal surface of the frontal bone, but continues on its undersurface far into the orbit, and that the orbitosphenoid and parasphenoid contact each other and the rhinosphenoid is absent.

In *Brycon*, as in *Acestrorhynchus* and *Piaractus*, the ribs on the fifth centrum (the first "normal" pair of ribs) bear strong, medially-directed processes which serve as broad bases for ligamentous attachment of the ossa suspensoria, the modified ribs of the fourth centrum. Similar processes are apparently also present in *Alestes leuciscus* and *A. baremose* (Monod, 1950, figs. 101, 103) but have not been found in any characoids outside of the family Characidae. Such processes are absent in *Salminus*, and in lacking them *Salminus* is perhaps more primitive than most other Characidae.

Brycon has three epurals whereas *Salminus* has but two. It is generally thought that the higher number of epurals is more primitive. Reduction from three to two and even to one has probably occurred independently in diverse lines of characoids, and sometimes, as in this instance, characoids otherwise primitive in many other respects have a reduced number of epurals.

CATABASIS

Catabasis acuminatus Eigenmann and Norris (1900) from the Rio Tieté, Paraná basin, in southeast Brazil, represents a monotypic genus supposed by its authors to be related to *Salminus* but differing in the disposition of its teeth. They described its teeth in the following terms:

Não tem dentes no palato. Queixada inferior com uma serie dupla de dentes; os da serie interior são exiguos e os da exterior são grandes e conicos, regularmente diminuindo em tamanho do segundo dente a partir da symphysis para traz. Os dentes do intermaxillar formam uma serie dupla, os da serie exterior são exiguos e os da serie interior são curtos e conicos

(Eigenmann and Norris, p. 358).

The only known specimen of *Catabasis*, the 165 mm. holotype of *C. acuminatus*, is in the fish collection of the California Academy of Sciences (catalog number CAS 11894, formerly IUM 9262). I have examined the teeth of this specimen without finding any evidence that they were derived from multicuspoid teeth, i.e., all of the teeth are conical and none have vestigial cusps. Many of the teeth are damaged, however, and what appear to be worn cusps on some of them are due to broken or chipped surfaces. The number of teeth is fewer than in any species of *Salminus*. The right premaxillary has seven teeth in the external tooth row and five teeth in the internal row (the left premaxillary has been torn away). The right maxillary bears about 24 teeth and the left maxillary about 19 (tooth rows of both maxillaries slightly damaged). The right dentary has 11 teeth in the external row and the left dentary has ten; the anterior portions of the internal tooth rows of both dentaries have been lost along with the gum which has been torn out. The internal tooth row of the left dentary is intact further anteriorly than that of the right dentary; the intact portion of the internal tooth row of the left dentary commences inside the fourth tooth of the external tooth row. It is impossible to tell whether the internal tooth row continued anteriorly to near the symphysis, as it does in *Salminus*.

The head and body of *Catabasis* are more compressed than in *Salminus*, and the snout is relatively more pointed; hence in general habitus *Catabasis* resembles *Brycon acutus* and *Acestrorhampus* more than *Salminus*. In *Salminus* and *Brycon* the posterior portion of the maxillary bone slips partially beneath the first and second circumorbital bones when the fish's mouth is closed, whereas in *Catabasis* the posterior portion of the maxillary has a dorsally directed flange which lies external to the circumorbital bones.

Catabasis is unquestionably a distinct genus of Characidae. Whether it is closely related to *Salminus* is uncertain; perhaps young specimens of *Catabasis* will reveal phylogenetically significant ontogenetic changes in dentition.

REMARKS ON *BRYCON ACUTUS* BÖHLKE

Brycon acutus Böhlke (1958, pp. 67-69, pl. 4, fig. 1), from the Rio Esmeraldas basin of western Ecuador, is slenderer and more compressed than typical *Brycon*, and its jaws are much more elongate. As noted by Böhlke, the wide spacing and relatively enlarged central cusps of the anterolateral tricuspid lower jaw teeth distinguish it from all other species of *Brycon*. Two large specimens in the Stanford collection (SU 22773, 172 and 190 mm. in standard length) from "Naranjito, Ecuador" (= Rio Naranjal?) are tentatively identified as adults of this species. They have been compared with the holotype and a paratype of *B. acutus*, and agree in all essential respects except that they are relatively even more compressed than typical *Brycon* of comparable size, and their dental peculiarities are more pronounced. As in the type material of *B. acutus*

(63.3 to 89.5 mm. in standard length) the third and fourth mandibular teeth are the largest, but their tricuspid nature is not readily apparent. Functionally they are conical teeth; the anterior and posterior cusps are indicated by worn ridges on the leading and trailing edges of the greatly enlarged central cusp. The mandibular teeth anterior to these teeth have five cusps and those posterior to them have three cusps; in all of these teeth the central cusp is enlarged and the other cusps are reduced in size. The single conical tooth of the internal mandibular row near the symphysis is reduced. The internal mandibular row is represented in the posterior portion of the jaw by a series of about a half dozen very small conical teeth.

SPACING OF THE JAW-TEETH IN CHARACOIDS

The peculiar spacing of the teeth in *B. acutus* leads me to make the following speculations. Elongation or foreshortening of the jaws in the course of phylogeny may sometimes have a direct effect on the spacing of the jaw-teeth in fishes. That this phenomenon appears to be particularly pronounced in characoids is perhaps related to their mode of tooth replacement by preformed replacement teeth. It occurs most often when the teeth involved are obsolescent or relatively unimportant functionally, such as the teeth on the maxillary bone beyond the gape of the mouth, but functionally important teeth may also be involved.

Many instances of what can be regarded as crowding out of teeth from an originally straight row or rows of teeth can be cited among characoids, and this is probably often due to a secondary shortening of the jaws. This has apparently happened in *Piabucus*, in which each premaxillary bears a single small tooth external to the main uniserial row of teeth for which it is difficult to imagine any functional significance. Rowntree (1906, p. 240, fig. 1) states that these two supernumerary teeth appear from their size and position to be quite useless, and their form does not show the symmetrical perfection of the functional teeth, although they are of the same general type.

Wider spacing of the jaw-teeth has apparently resulted from secondary elongation of the jaws. *Brycon acutus* is one such example; an even more striking example is provided by the highly specialized genus *Catoprion*, the teeth of which are accurately illustrated by Müller and Troschel (1845, pl. 2, fig. 5). *Catoprion* strongly resembles *Serrasalmus*, to which it is closely related; according to Gosline's suggested phylogeny of the Serrasalmoninae (Gosline, 1951, fig. 4, p. 25) they are the more or less direct descendants of a common ancestor. In *Serrasalmus* the jaw-teeth are very close-set and actually form an interlocking series (Roberts, 1967a, fig. 4). The morphology of the teeth in the peculiarly elongated jaws of *Catoprion* differs in only minor respects but they are spaced wide apart.

RELATIONSHIPS OF *ACESTRORHYNCHUS*

According to Weitzman (1964, p. 135), the relationships of *Acestrorhynchus* and *Acestrorhamphus* probably lie with *Charax*, *Roeboides*, and other closely related genera in the Characidae, not with *Boulengerella* and *Ctenolucius* as supposed by Gregory and Conrad (1938). In partial confirmation of this statement, there is nothing in the osteology of the Ctenoluciidae and of *Acestrorhynchus* to indicate that they are closely related. Such similarities as exist between them are superficial and must be credited to convergent evolution. Superficially at least, *Charax* and *Roeboides* resemble *Acestrorhynchus*. Unfortunately *Acestrorhynchus* cannot be compared osteologically with these genera because their osteology is as yet unknown.

The relationships of *Acestrorhynchus*, *Roeboides*, *Charax*, and other, apparently related, specialized genera with rapacious conical dentition (for a review of the genera involved see Géry and Vu-Tân-Tuê, 1963) to other sections of the Characidae remains problematical. Up to now there has been no strong evidence that *Acestrorhamphus* and *Acestrorhynchus* are directly related to characids with multicuspid teeth. Evidence for such a conclusion can now be supplied by specimens of *Acestrorhamphus* "*hepsetus*" from Argentina (SU 31566) which have multicuspid teeth on the posterior portion of the jaws.

I previously reported (Roberts, 1967) that the teeth are all conical and do not show any sign of being multicuspid in *Acestrorhynchus*, even in very small specimens. Re-examination of some small *Acestrorhynchus* reveals no multicuspid teeth (although there is an internal mandibular row of small conical teeth in the posterior part of the jaw which is lacking in adults). The young *Acestrorhynchus* examined represent a specialized species with very elongate jaws.

Acestrorhamphus is apparently closely related to *Acestrorhynchus* but differs from it in having a uniserial row of relatively large conical teeth on the ectopterygoid bone instead of far more numerous and irregularly arranged teeth, in retaining multicuspid teeth on the posterior portion of the jaws particularly in the young, and in having a more generalized, *Brycon*-like habitus which is at least superficially similar to that of *Brycon acutus* and *Bramocharax*. In all of these respects *Acestrorhamphus* is probably more primitive than *Acestrorhynchus*; it is apparently still generalized enough that it could have given rise directly to *Acestrorhynchus*.

In adult *Acestrorhamphus* all of the teeth within the gape of the mouth are conical but the teeth on the posteriormost portion of the maxillary extending beyond the gape are multicuspid. Although the lateral cusps of these teeth may be obsolescent, they are definitely present. In half-grown specimens, tricuspid teeth are present on the posterior portion of the dentary as well as on the maxillary, and the lateral cusps are relatively well developed. *Acestrorhamphus* provides a striking example of the generalization that specialized characoids some-

times retain primitive teeth on the posteriormost portions of their jaws (Roberts, 1967a).

REMARKS ON AFRICAN CHARACIDAE

Certain morphological features shared by all or by many of the African Characidae, which represent a far smaller and more closely related group of genera than the American Characidae, indicate that they are separable from the latter at the subfamily level. African characids, as pointed out to me by Professor Myers, have a characteristic shape of the upper jaw which is quite unlike that in American genera. In almost all of them—including *Alestes baremose*, *A. grandisquamis*, *A. imberi*, *A. liebrechtsii*, *A. macrolepidotus*, *Bryconacthiops*, *Micralestes occidentalis*, and *Phenacogrammus interruptus*—the premaxillary has a slender, pedicle-like posterior process extending laterally to the maxillary bone, with which it is frequently rather firmly united. The maxillary in African characids is invariably toothless, and usually the posterior portion of the maxillary near the rictus of the jaws is an expanded lamella with a rounded ventral contour. In American characids the maxillary frequently bears teeth and its ventral margin is usually straight or else concave in varying degrees. The description of the peculiar molariform premaxillary teeth of *Alestes baremose* given earlier, with minor changes, would fit almost all of the larger species of African Characidae. Similar teeth are not present in American characids.

In American Characidae, as in characoids generally, the olfactory nerve arises from the orbitosphenoid and passes through the anterior portion of the orbit into the nasal organ through a foramen in the lateral ethmoid bone. In many African Characidae, however, this portion of the olfactory nerve is enclosed in a bony tube formed largely by the orbitosphenoid but often with a contribution from the lateral ethmoid. Bony tubes of this nature were first described by Starks (1926, p. 167) in *Alestes liebrechtsii* and *A. grandisquamis*; they are also present in *A. baremose*, *A. imberi*, *A. macrolepidotus*, *Bryconacthiops*, and *Hydrocynus*. In these fishes the bony tube is swollen about midway between its origin and the base of the lateral ethmoid; in alcoholic specimens it can be observed that this swelling is occupied by a thickened portion of the olfactory nerve. This thickening is presumably the olfactory bulb, which in other characoids usually lies immediately anterior to the lobes of the forebrain. In the relatively small specimens of *A. baremose*, *Micralestes*, and *Phenacogrammus* I have examined, although the orbitosphenoid does not form a well developed tube, it is somewhat modified anteriorly in a manner suggestive of the more complex development found in larger specimens of Alestiinae. Monod (1950, figs. 96, 97, p. 42) has figured a specimen of *A. baremose* in which the olfactory nerve has a complete bony enclosure that is apparently derived mainly from the orbitosphenoid bone, and a specimen of *A. leuciscus* in which the olfactory nerve

lies exposed in the orbit before entering the nasal chamber by passing through a foramen in the lateral ethmoid.

Two subfamilies of African Characidae are recognizable, the Alestiinae and the Hydrocyninae. The Alestiinae include all of the genera excepting the tiger-fishes of the genus *Hydrocynus*, which constitute the Hydrocyninae. *Hydrocynus* very probably had *Alestes*-like ancestors.

CONCLUSIONS

1. Osteological differences between the various families of characoids recognized by Greenwood and others (1966) are, on the whole, great enough to justify full familial rank.

2. The family Hepsetidae (represented by a single extant species in Africa) is phylogenetically isolated and is apparently the most primitive of all living characoids, even though it has its own peculiar specializations.

3. The family Ctenoluciidae (comprising the American genera *Ctenolucius* and *Boulengerella*) is a distinctive family which may be related to Hepsetidae. Its members are highly specialized in certain respects (notably jaw structure) and lack several bones of an apparently primitive nature which are present in *Hepsetus* (toothed dermopalatine or accessory ectopterygoid, lamellar canal-bearing supraopercle and antorbital bones).

4. The Erythrinidae are a small group of closely related fishes which appear to be primitive in certain respects and highly specialized in others. They are the only characoids besides *Hepsetus* known to have either an accessory ectopterygoid or a lamellar supraopercle, yet their many peculiar features (notably the structure of the pectoral girdle) clearly indicate that they represent a distinct family. The erythrinids are apparently too specialized to have given rise to any other group of characoids now in existence.

5. *Salminus* is a generalized characid and is perhaps the only living member of its family which has conical teeth of a primitively conical nature.

6. The morphology of *Catabasis* is insufficiently known to determine whether it is closely related to *Salminus*.

7. *Acestrorhynchus* and the closely allied *Acestrorhamphus* are highly specialized representatives of the family Characidae and are descended from characids with multicuspid teeth.

8. The presence of a rhinosphenoid bone in members of the Cynodontidae may indicate that this extremely peculiar family was derived from Characidae, the only other family known to possess this bone.

9. The Anostomidae and Chilodontidae are distinguished from all other families of characoids in having multicuspid pharyngeal teeth. The more or less identical morphology of these teeth in the Anostomidae and Chilodontidae indicates that the two families are closely related, and perhaps they should be put together in a single family.

10. African and American characoids currently assigned to the family Characidae are similar enough osteologically to justify their retention in a single family.

11. The African Characidae comprise two endemic subfamilies, Alestiinae and Hydrocyninae. The single genus (*Hydrocynus*) in the latter subfamily was clearly derived from the Alestiinae.

12. Epibranchial organs have been reported in a number of characoids, and a bone topologically identical with the supramaxillary bone is present in a species of *Chilodus*. These structures have been found only in characoids belonging to highly specialized families in which all of the structures involved in feeding are greatly modified. In all probability they have originated independently and are analogous rather than homologous with similar structures bearing these names which are found in other groups of teleosts.

13. The Hepsetidae and Erythrinidae are the only characoids having an accessory ectopterygoid bone. In erythrinids this bone is very small and barely discernible at the anterior end of the ectopterygoid, with which it is intimately connected. The finely dentigerous surfaces of the accessory ectopterygoid and ectopterygoid proper are virtually contiguous. In *Hepsetus*, on the other hand, the accessory ectopterygoid is relatively large and is clearly distinct from the ectopterygoid. It bears large teeth whereas the ectopterygoid itself is toothless. The accessory ectopterygoid of characoids may be homologous with the dermo-palatine bone in *Amia*.

14. In primitive characoids (typified by *Hepsetus*) the cranium has a flattened or only slightly vaulted roof and its dorsolateral margin is more or less straight. The dilator groove, or fossa for attachment of the *m. dilator operculi*, lies entirely ventral to the cranial roof. The facial bones are all lamellar and relatively large, and the dorsal edges of the dorsalmost ones (nasal, supra-orbital, and sixth infraorbital bones) are firmly articulated for their entire lengths with the dorsolateral margin of the cranium. The supraopercle is a large, canal-bearing lamellar bone and lies immediately posterior to the enlarged sixth infraorbital bone.

15. In specialized characoids (typified by *Acetrorhynchus*) the cranial roof tends to be highly vaulted and the dilator groove may extend onto its dorsal surface. The dorsolateral cranial margin is disrupted and the facial bones are not so extensively or intimately articulated with it as in primitive characoids. Correlated with this, facial bones are lost or reduced in size. The supraopercle has been lost. Other facial bones may be reduced to mere segments of bony tubing for encasement of the laterosensory canals. Thus the soft tissues of the head are often relatively exposed in specialized characoids compared to those of primitive ones.

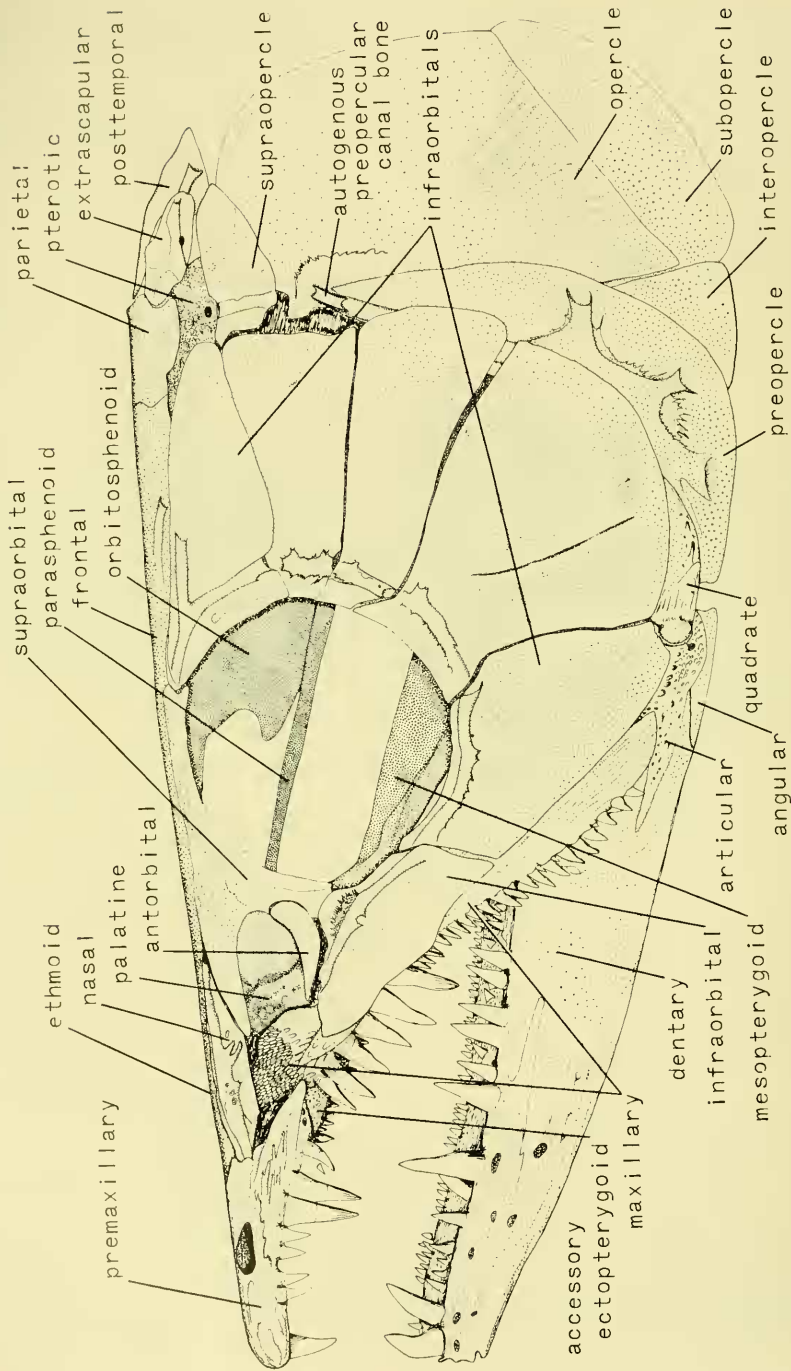


FIGURE 1. *Hepsetus odoe*, lateral view of skull.

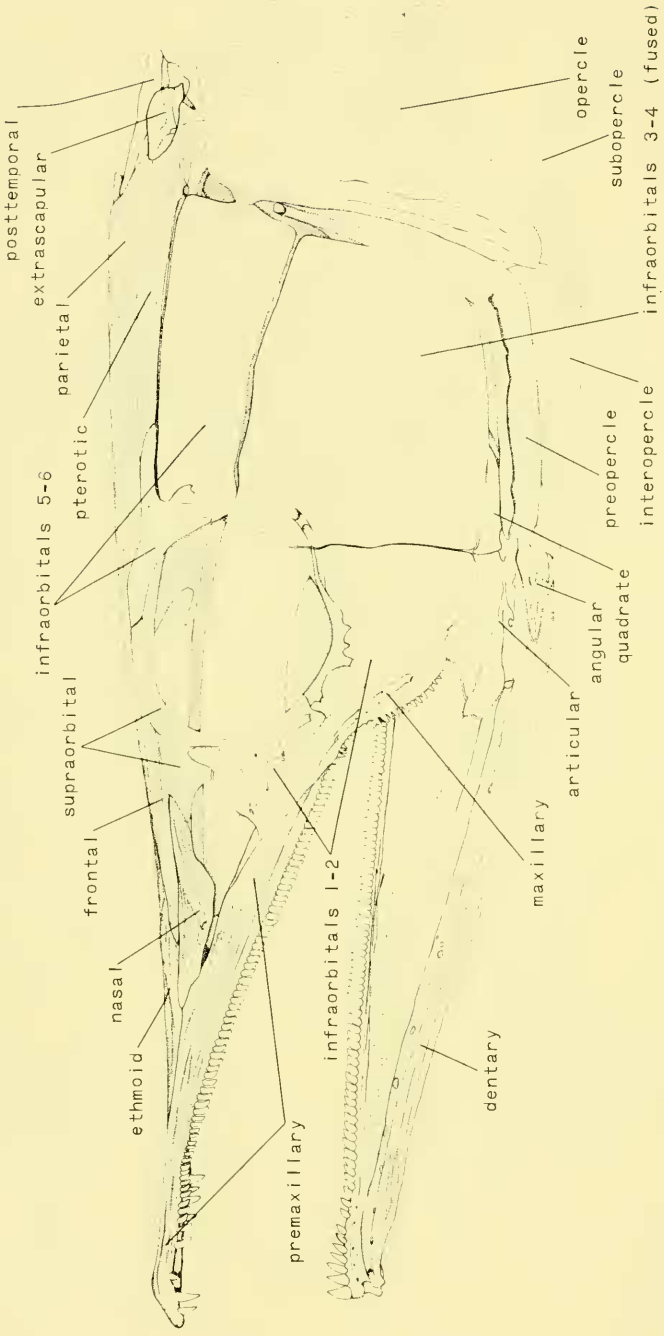


FIGURE 2. *Ttenolucius hujeta*, lateral view of skull.

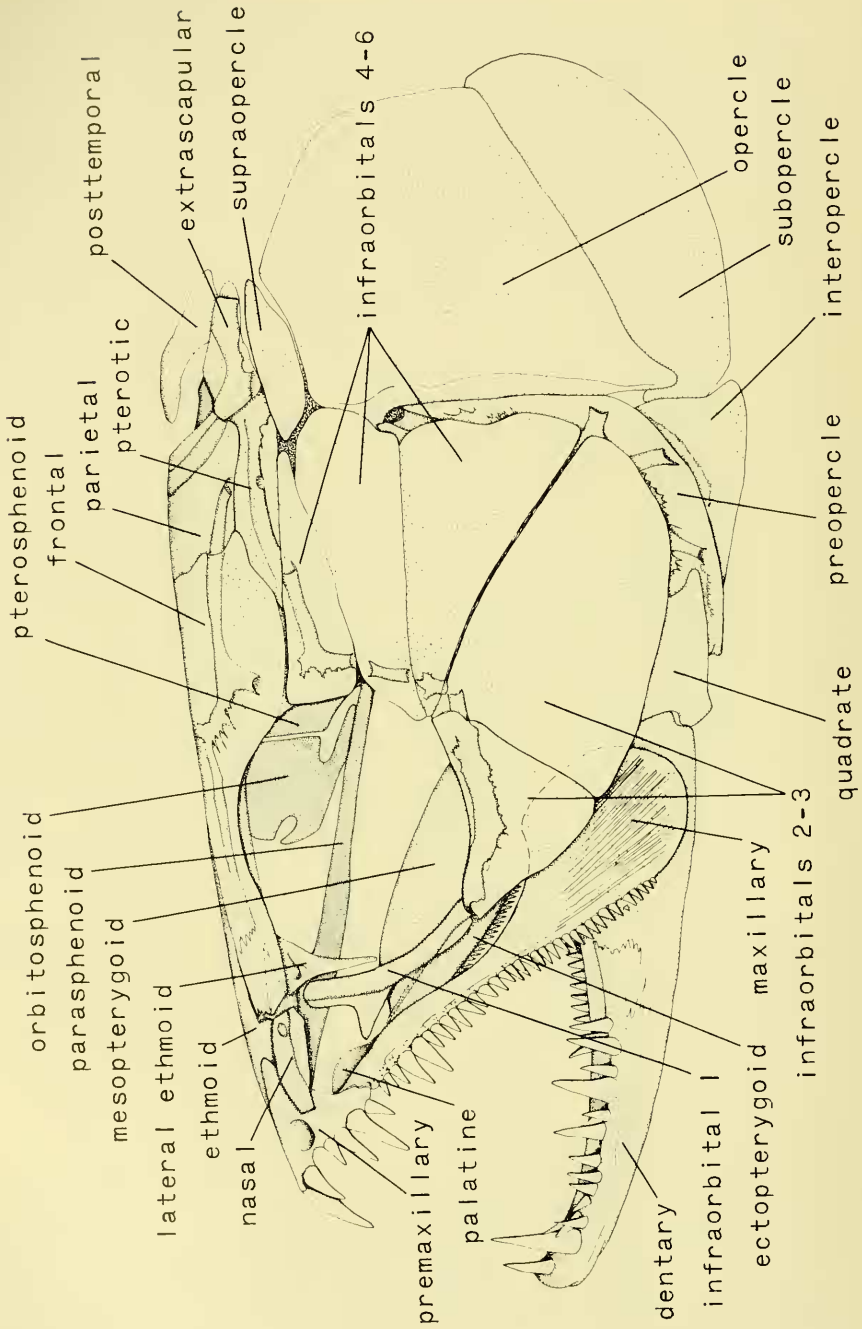


FIGURE 3. *Hoplias* species, lateral view of skull.

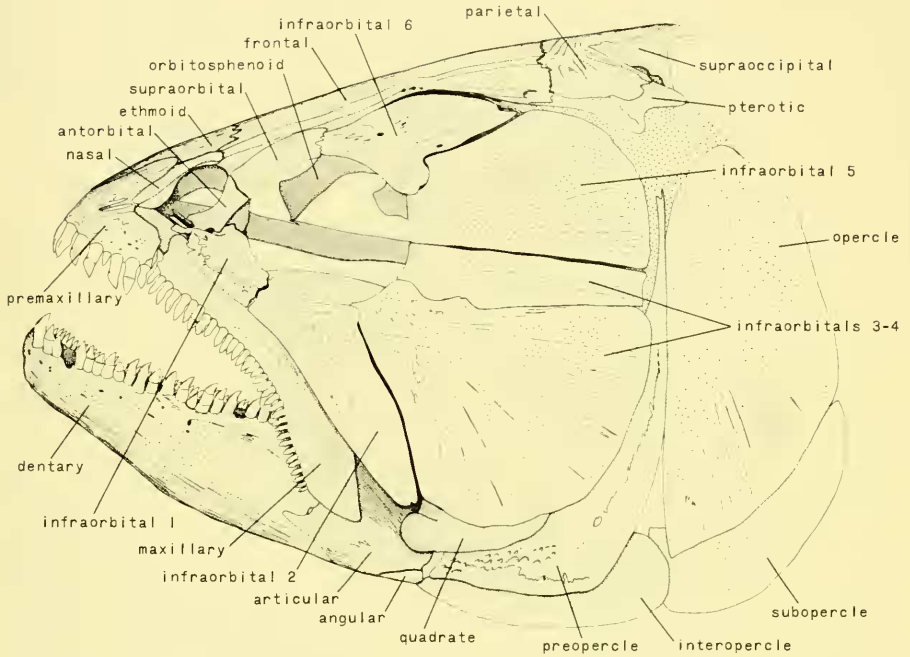


FIGURE 4. *Salminus brasiliensis*, lateral view of skull. There is a small anomalous bony structure (unlabeled) lying superficially to the anterior portion of the antorbital. It presumably served as investiture for the anteriormost portion of the infraorbital branch of the cephalic lateral line system. Such structure is usually lacking in *Salminus*, and one is not present on the other side of the head in the specimen figured.

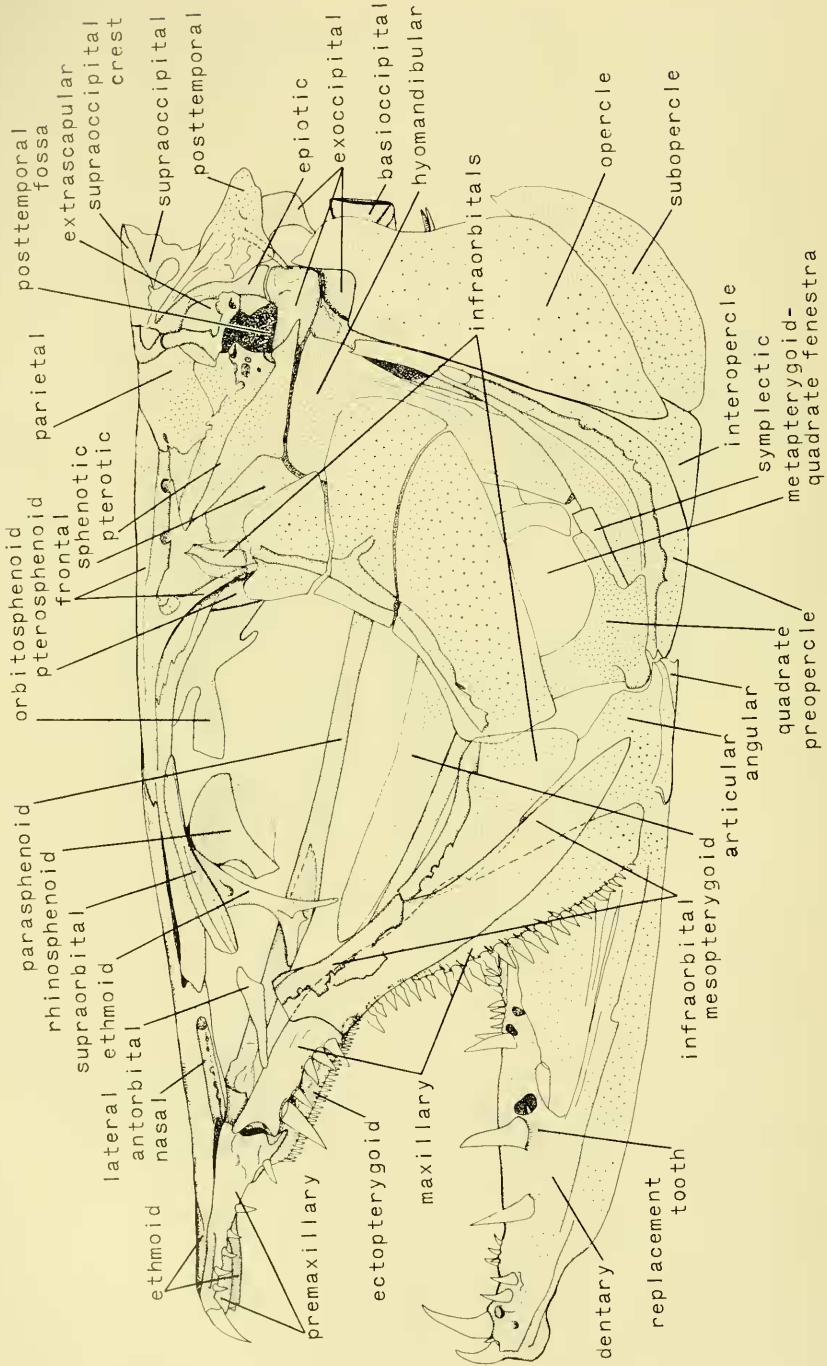


FIGURE 5. *Accestrorhynchus* species, lateral view of skull.

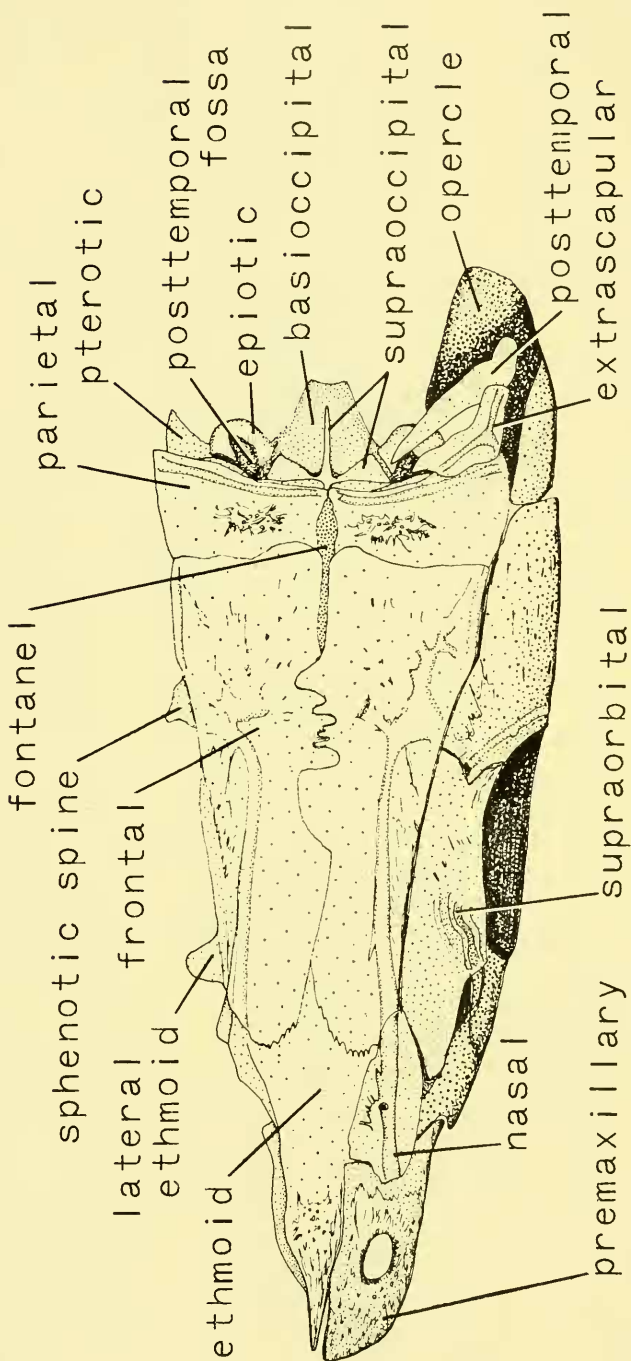


FIGURE 6. *Hepsetus odotae*, dorsal view of skull.

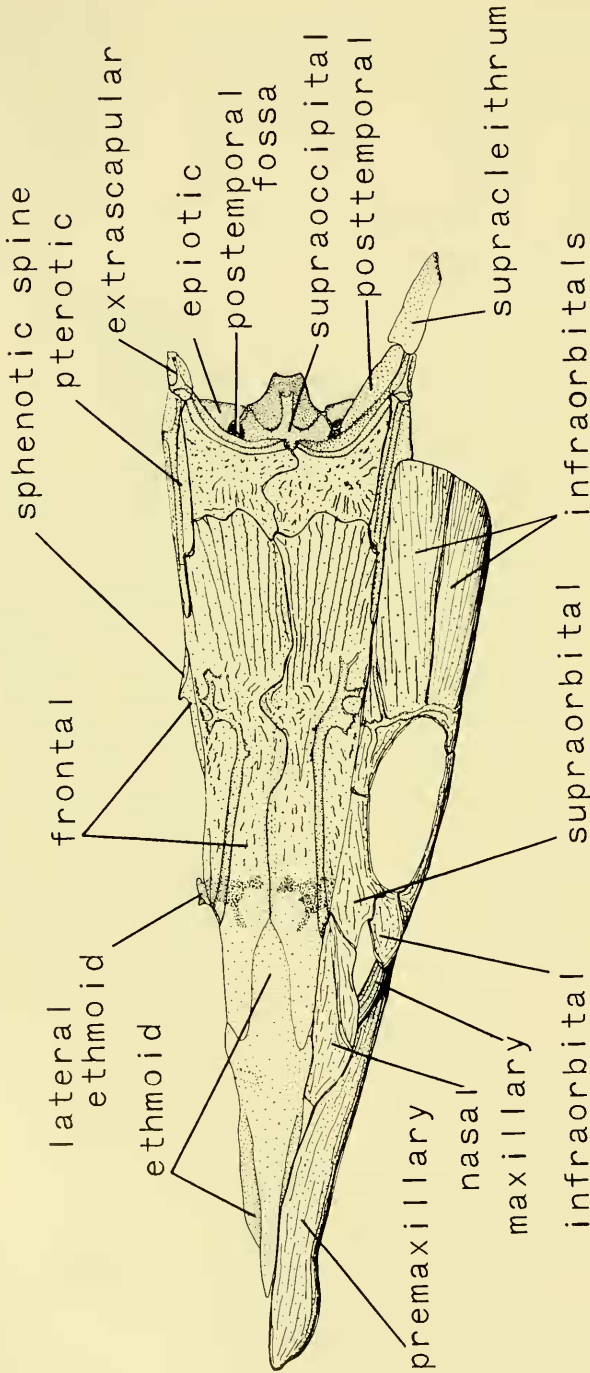


FIGURE 7. *Ctenolucius hujeta*, dorsal view of skull.

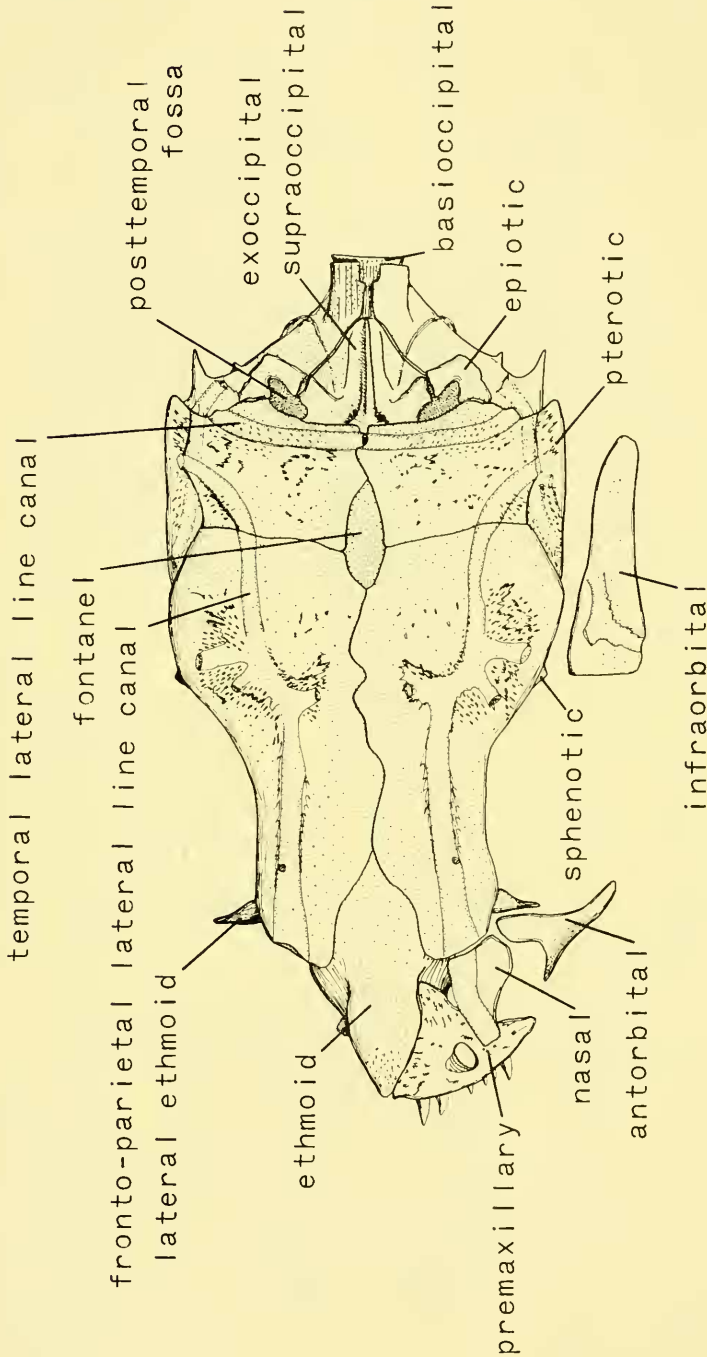


FIGURE 8. *Hoplias* species, dorsal view of skull.

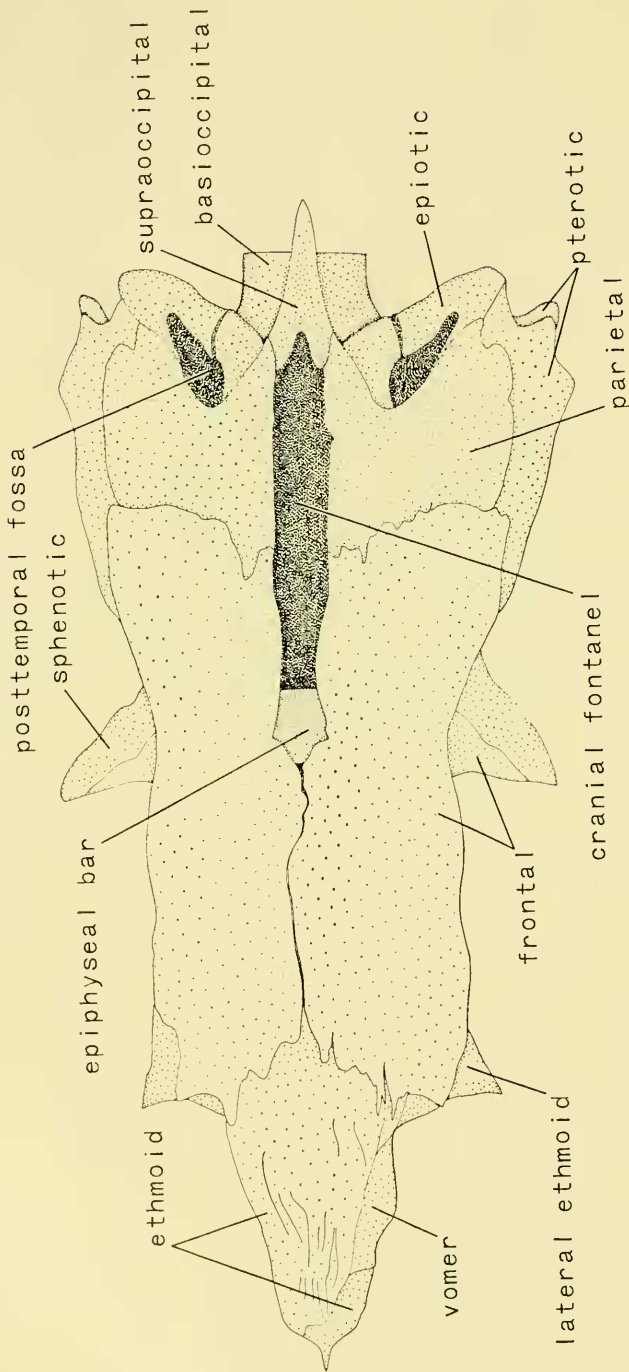


FIGURE 9. *Salminus brasiliensis*, dorsal view of skull. Superficial ridges and grooves and laterosensory canals not shown. Left side of ethmoid bone damaged.

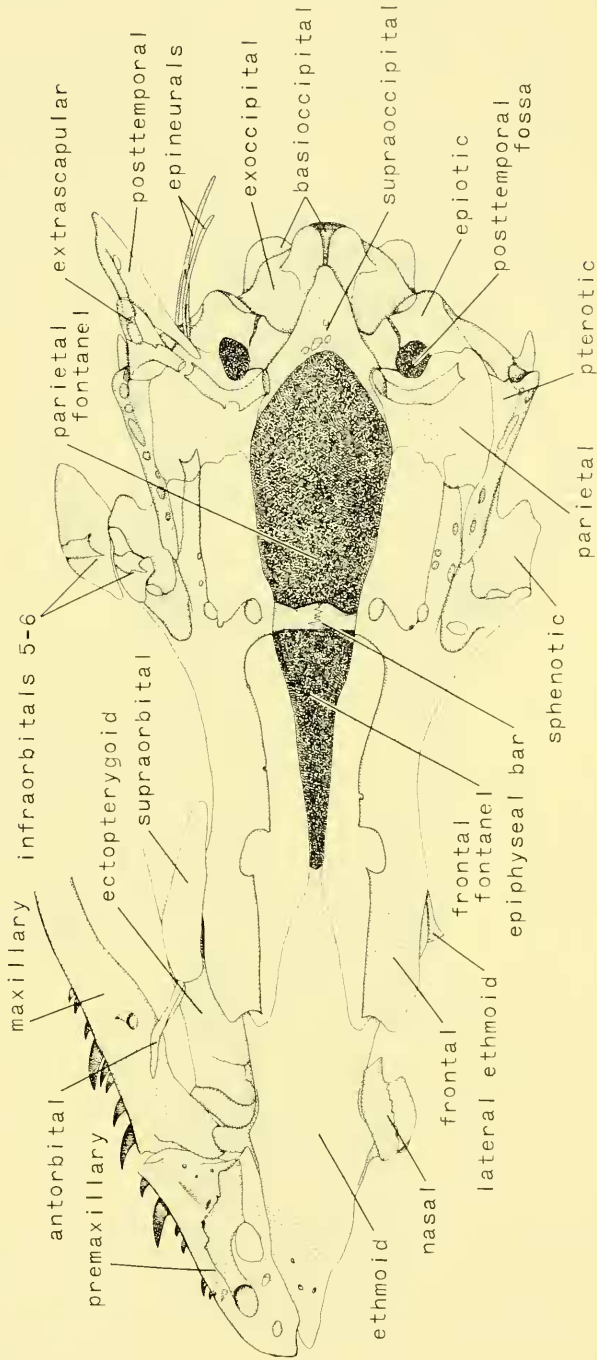


FIGURE 10. *Acetrorhynchus* species, dorsal view of skull.

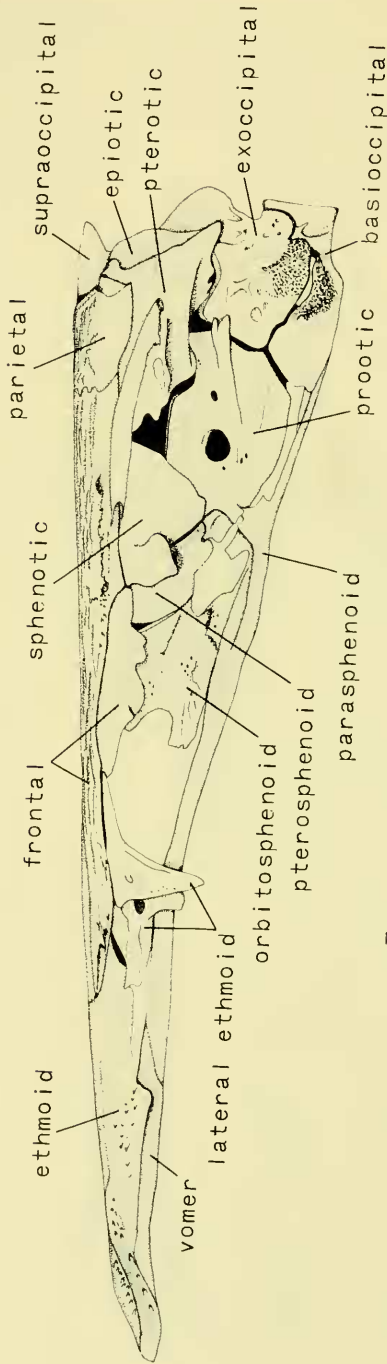


FIGURE 11. *Hepselus odoe*, lateral view of cranium.

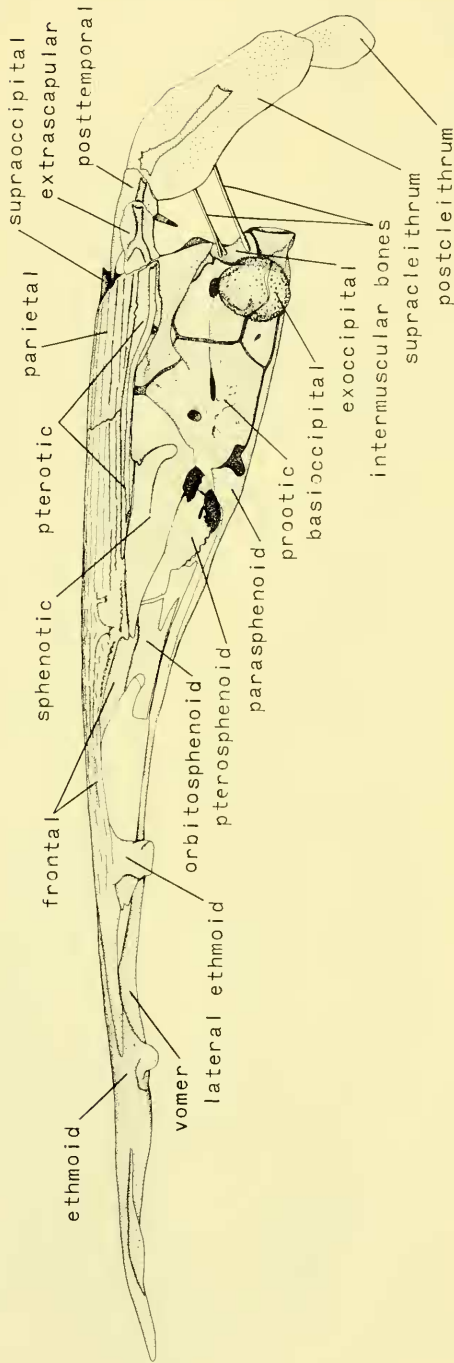


FIGURE 12. *Ctenolucius hujeta*, lateral view of cranium and secondary pectoral girdle.

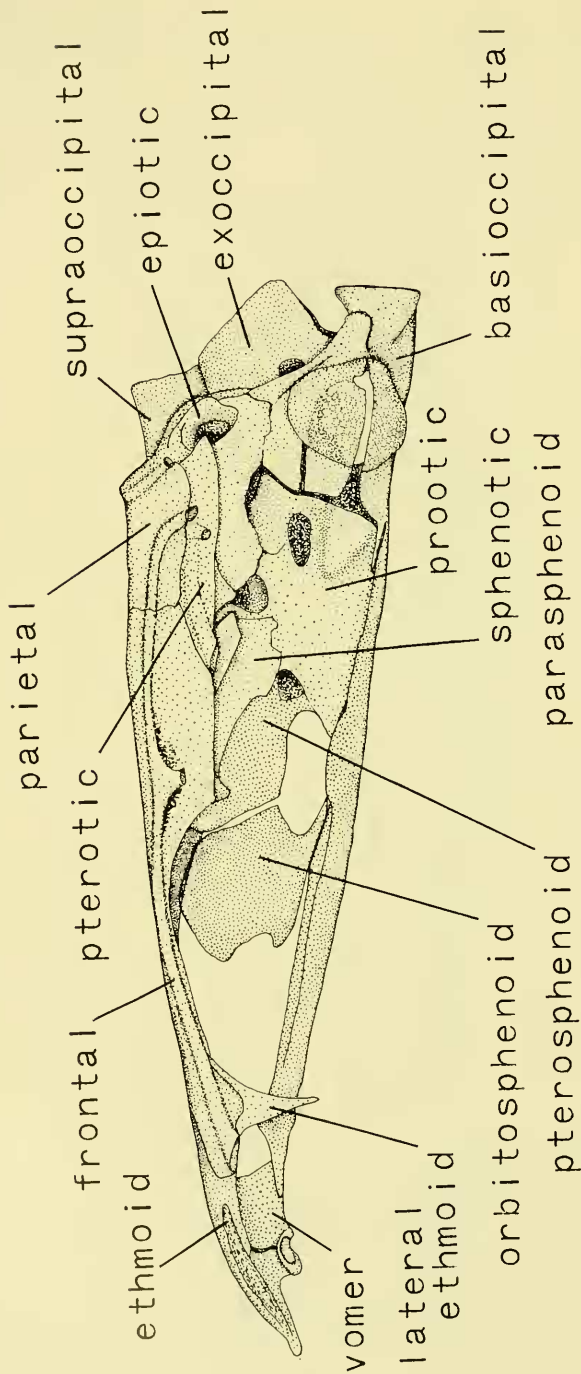


FIGURE 13. *Hoplias* species, lateral view of cranium.

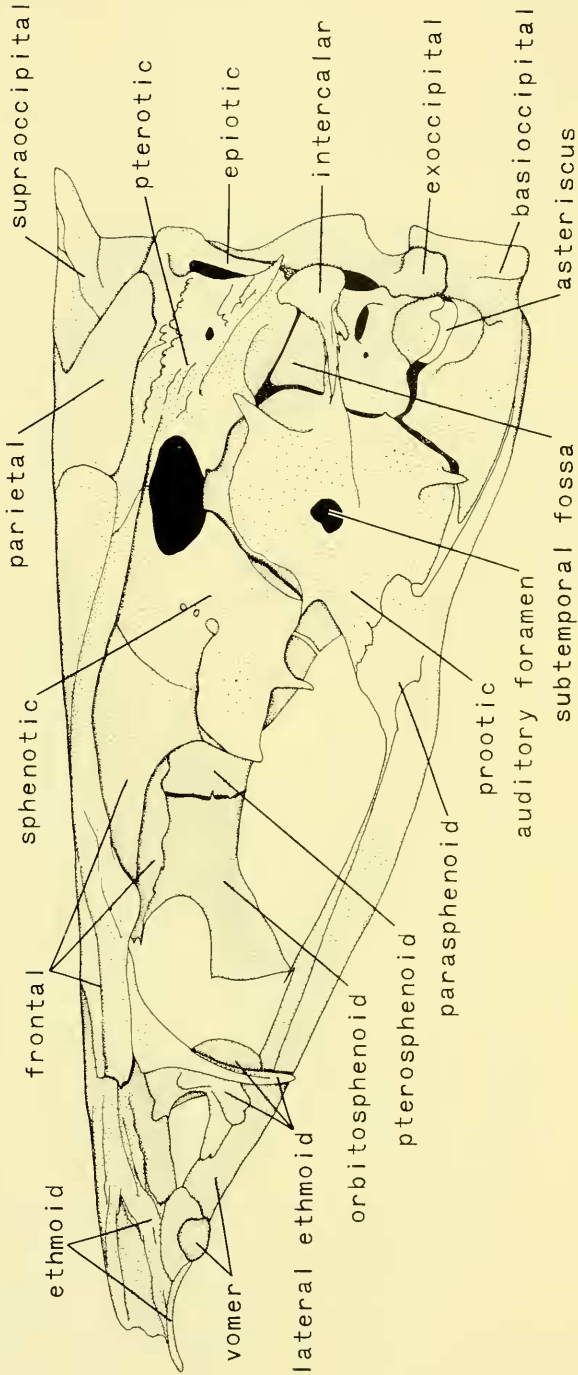


FIGURE 14. *Sabminus brasiliensis*, lateral view of cranium. Ethmoid bone damaged (see fig. 9).

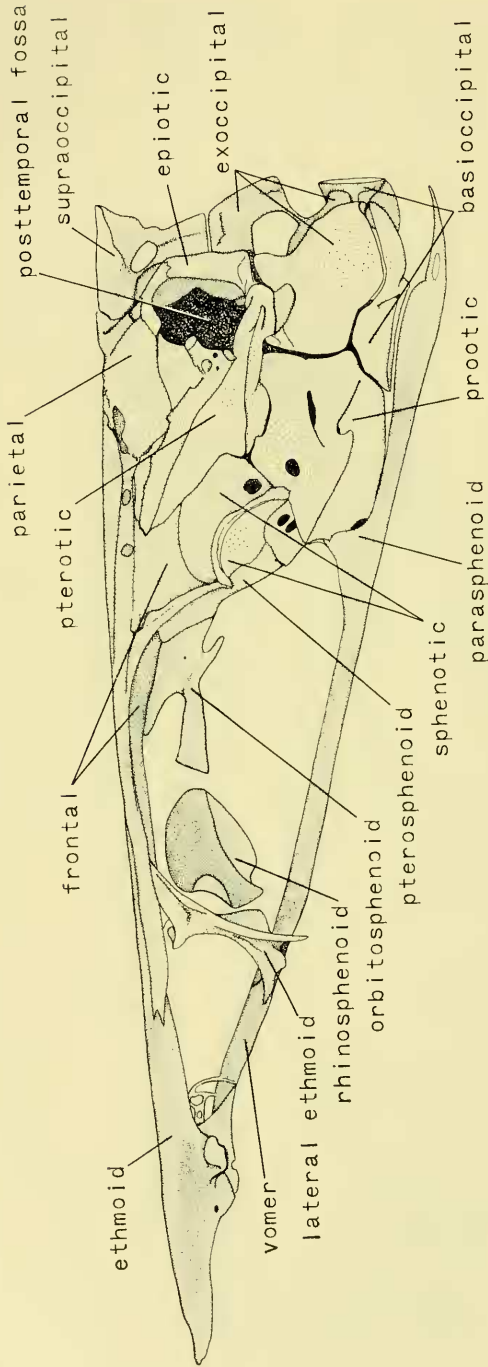


FIGURE 15. *Acetrorhynchus* species, lateral view of cranium.

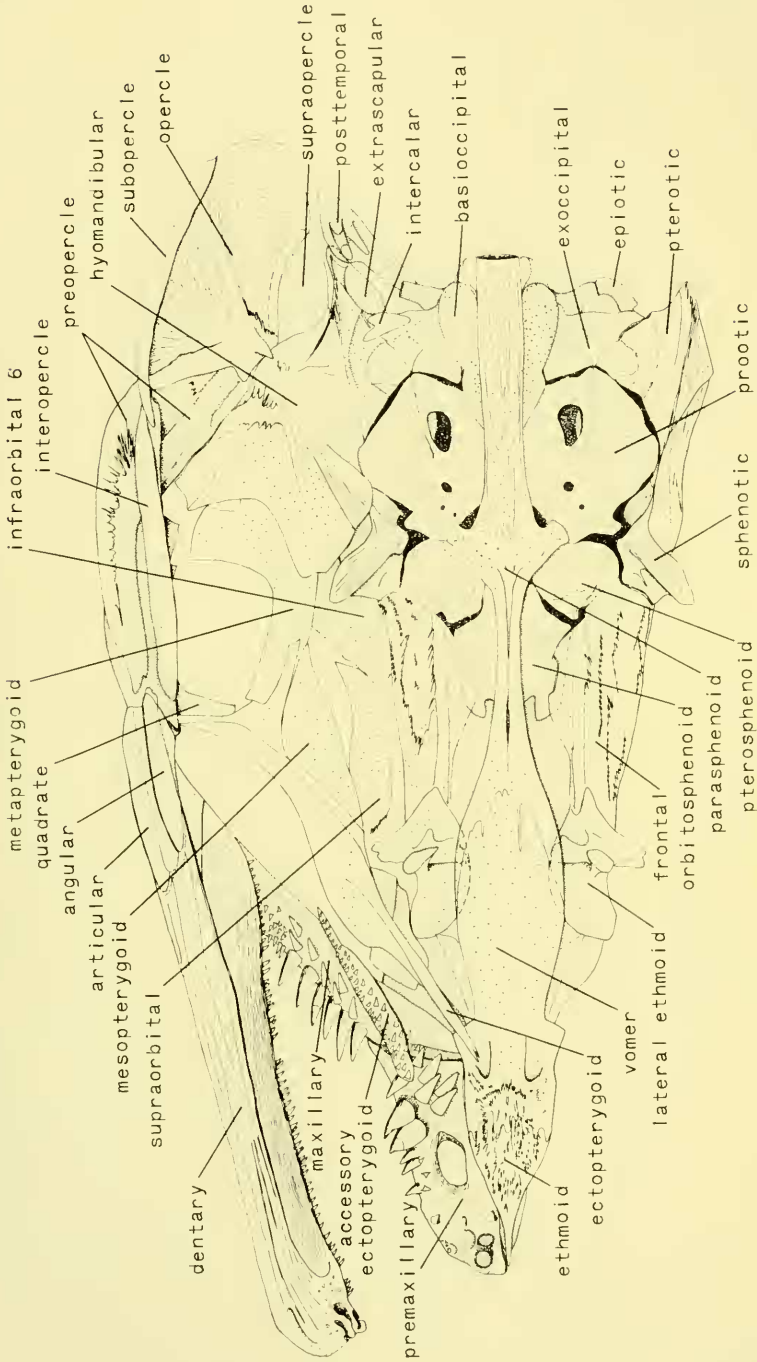


FIGURE 16. *Hepsetus odoe*, ventral view of cranium, with jaws and facial bones of left side attached.

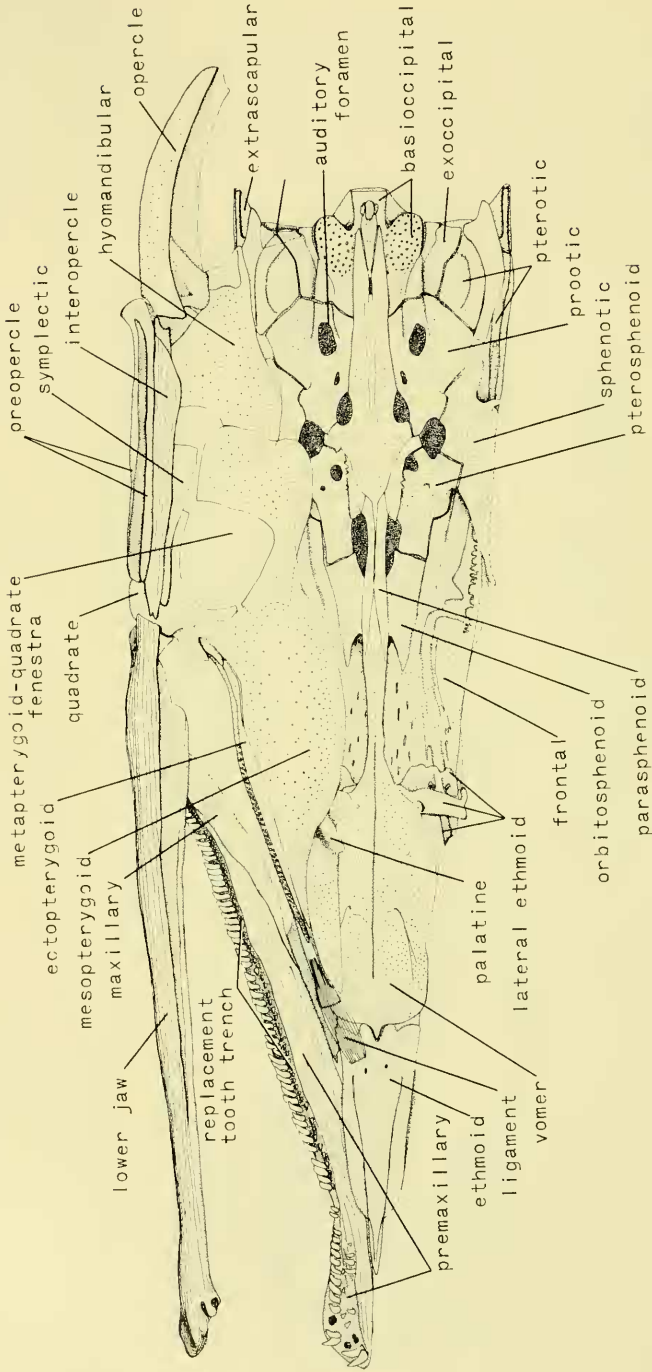


FIGURE 17. *Ttenolucius hujeta*, ventral view of cranium, with jaws and facial bones of left side attached (subopercle detached).

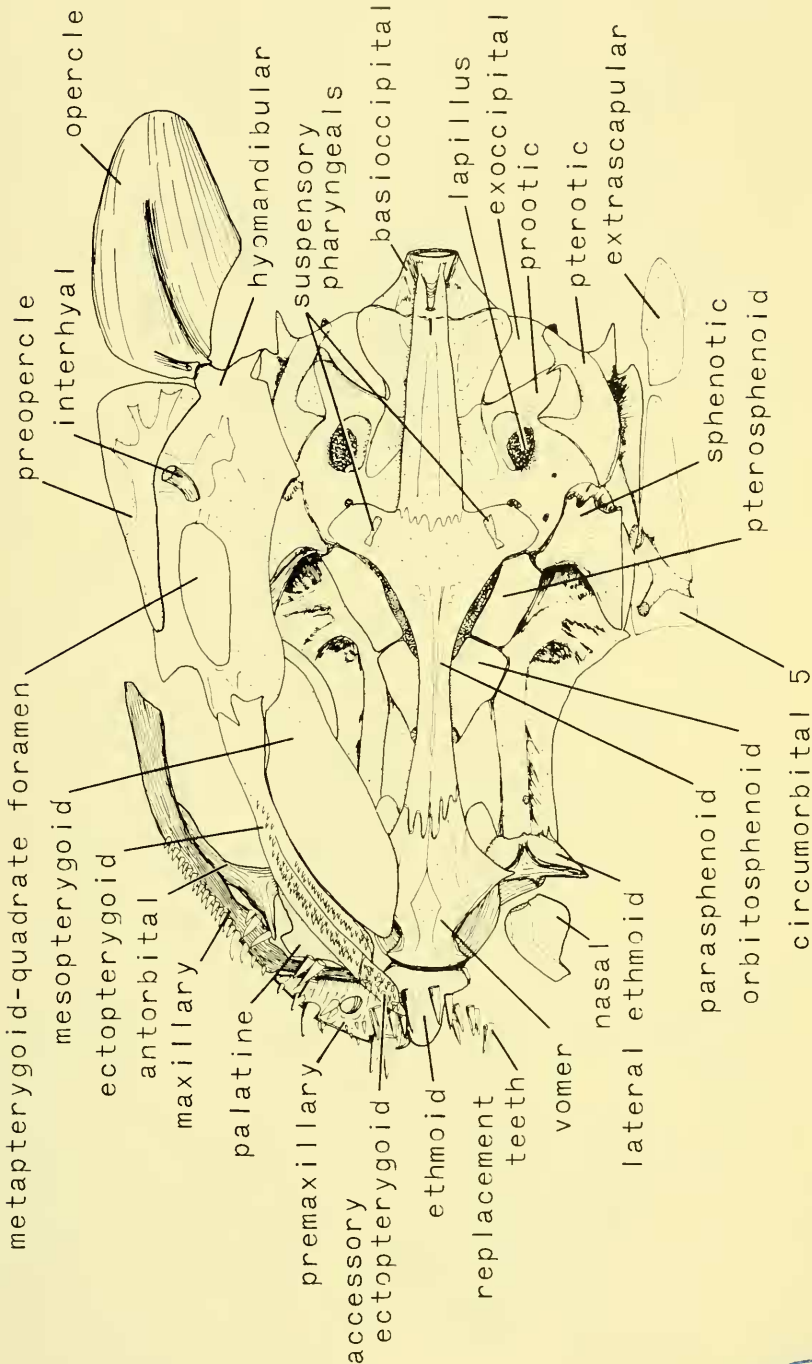
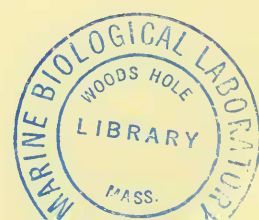


FIGURE 18. *Hoplias* species, ventral view of cranium, with portions of jaws and facial bones attached.



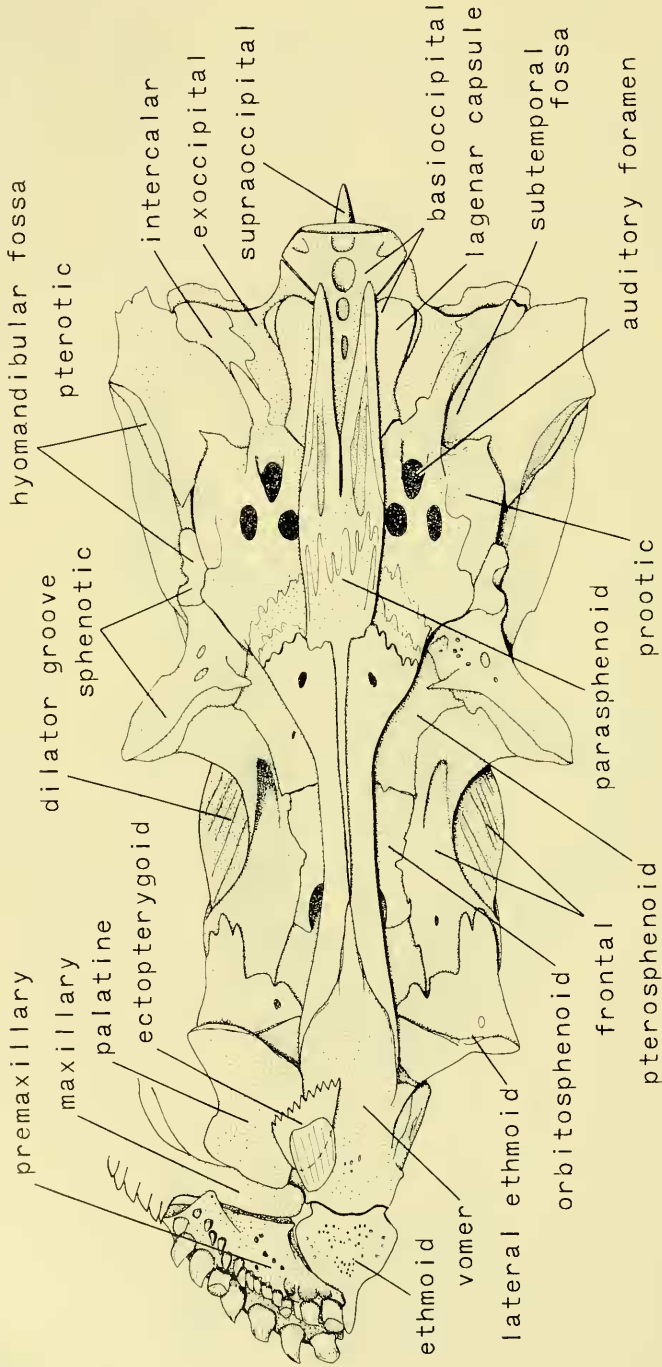


FIGURE 19. *Salminus brasiliensis*, ventral view of cranium, with jaws of left side attached.

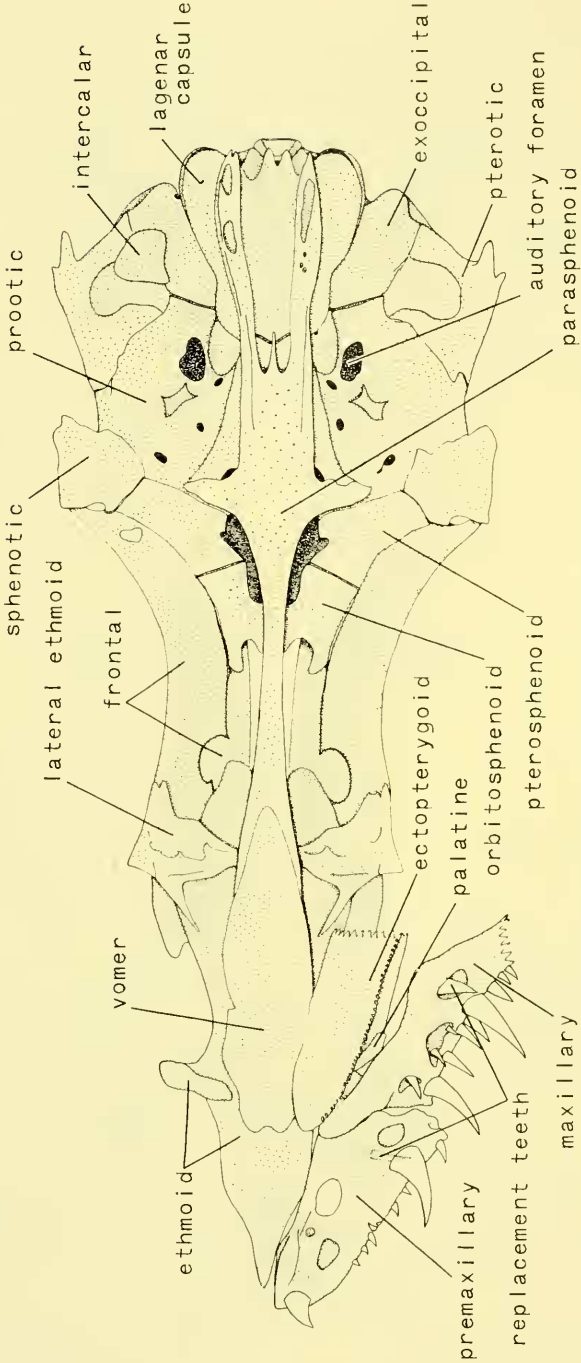


FIGURE 20. *Acetrorhynchus* species, ventral view of cranium, with jaws of right side attached.

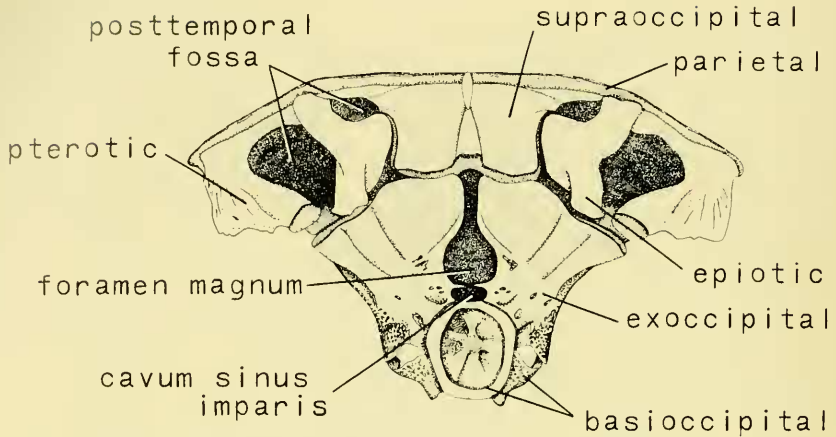


FIGURE 21. *Hepsetus odoc*, posterior view of cranium.

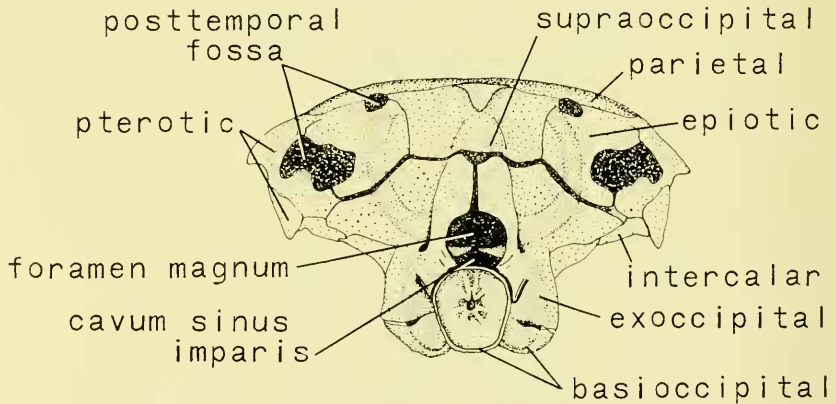


FIGURE 22. *Ctenolucius hujeta*, posterior view of cranium.

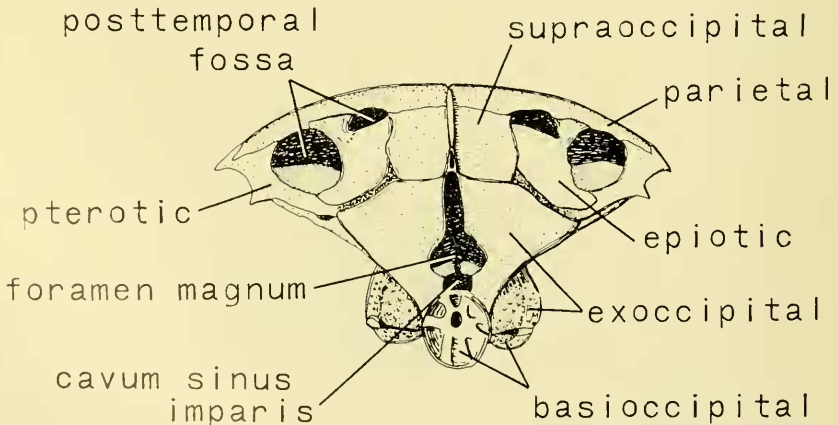


FIGURE 23. *Hoplias* species, posterior view of cranium.

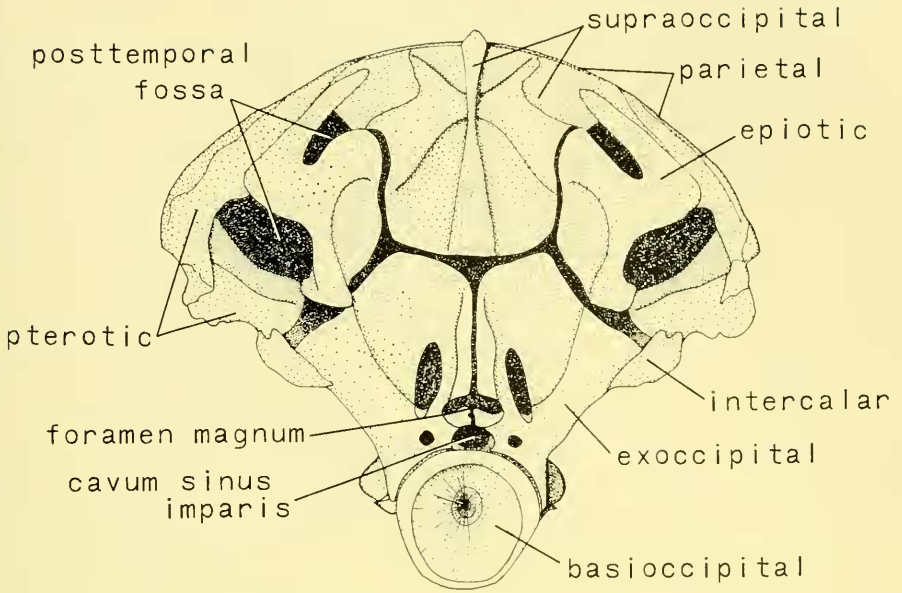


FIGURE 24. *Salminus brasiliensis*, posterior view of cranium.

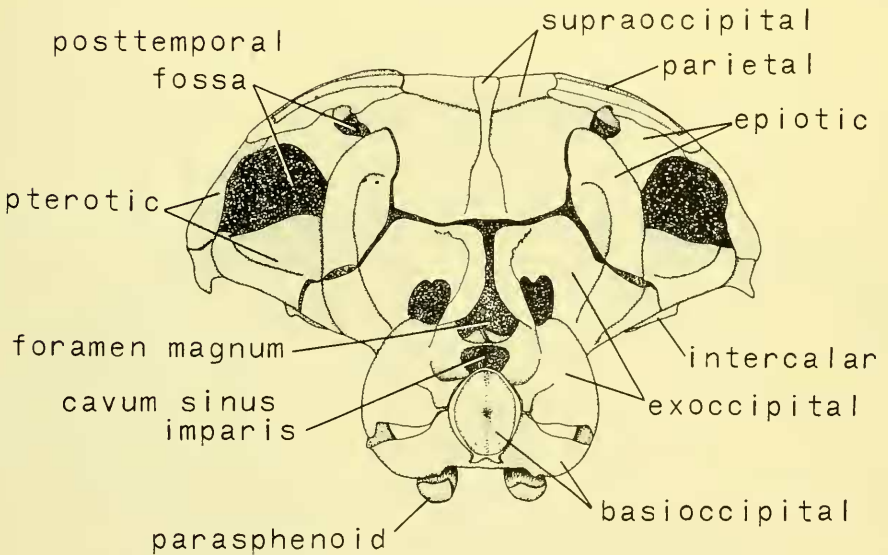


FIGURE 25. *Acestorhynchus* species, posterior view of cranium.

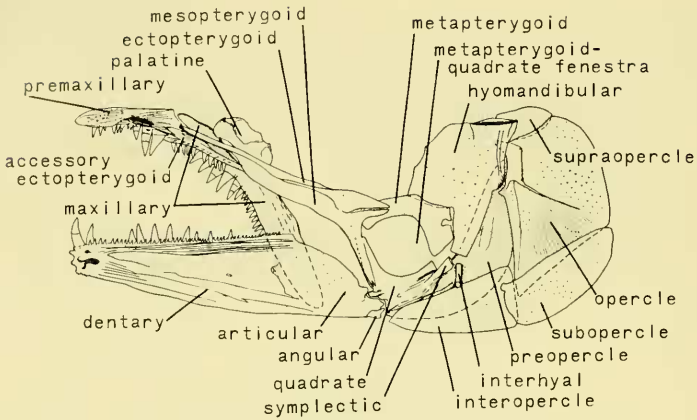


FIGURE 26. *Hepsetus odoe*, internal view of jaws and deeper facial bones.

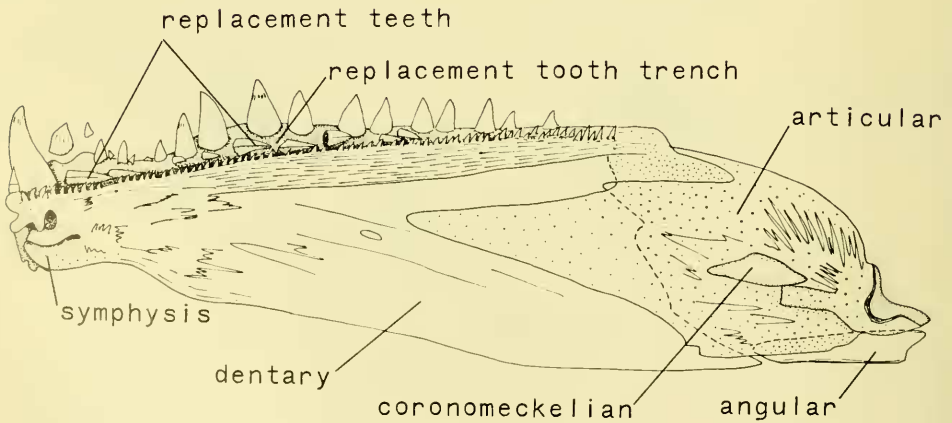


FIGURE 27. *Hepsetus odoe*, internal view of lower jaw.

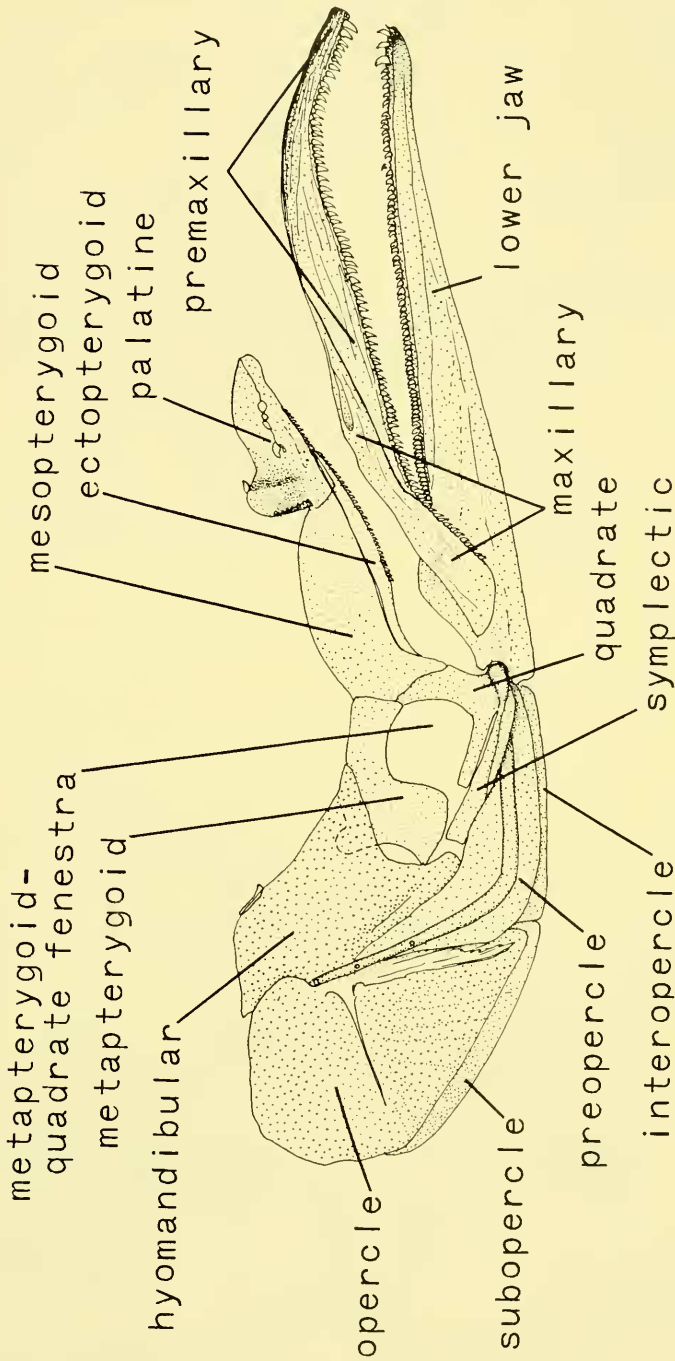


FIGURE 28. *Ctenolucius hujieta*, external view of jaws and deeper facial bones.

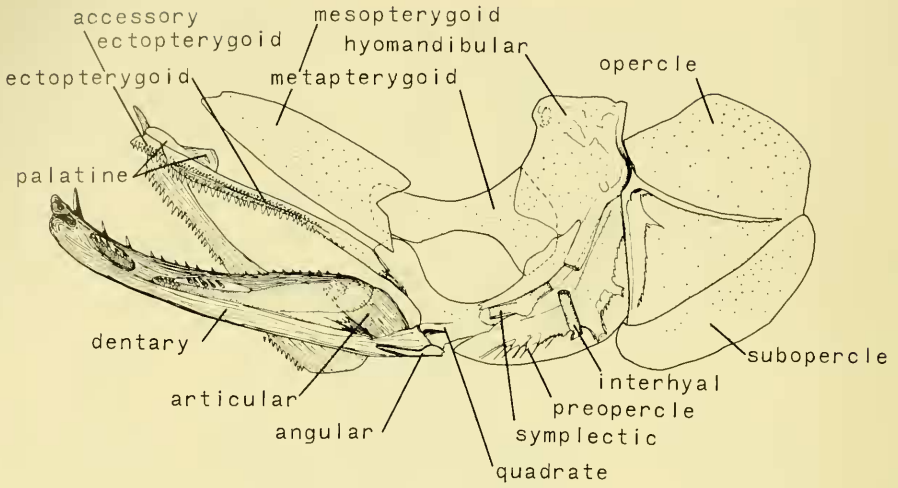


FIGURE 29. *Hoplias* species, internal view of jaws and deeper facial bones (premaxillary and interopercle detached).

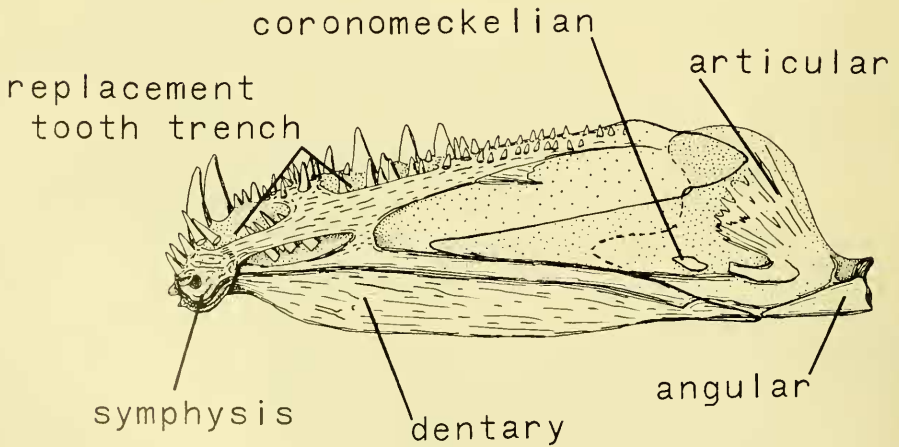


FIGURE 30. *Hoplias* species, internal view of lower jaw.

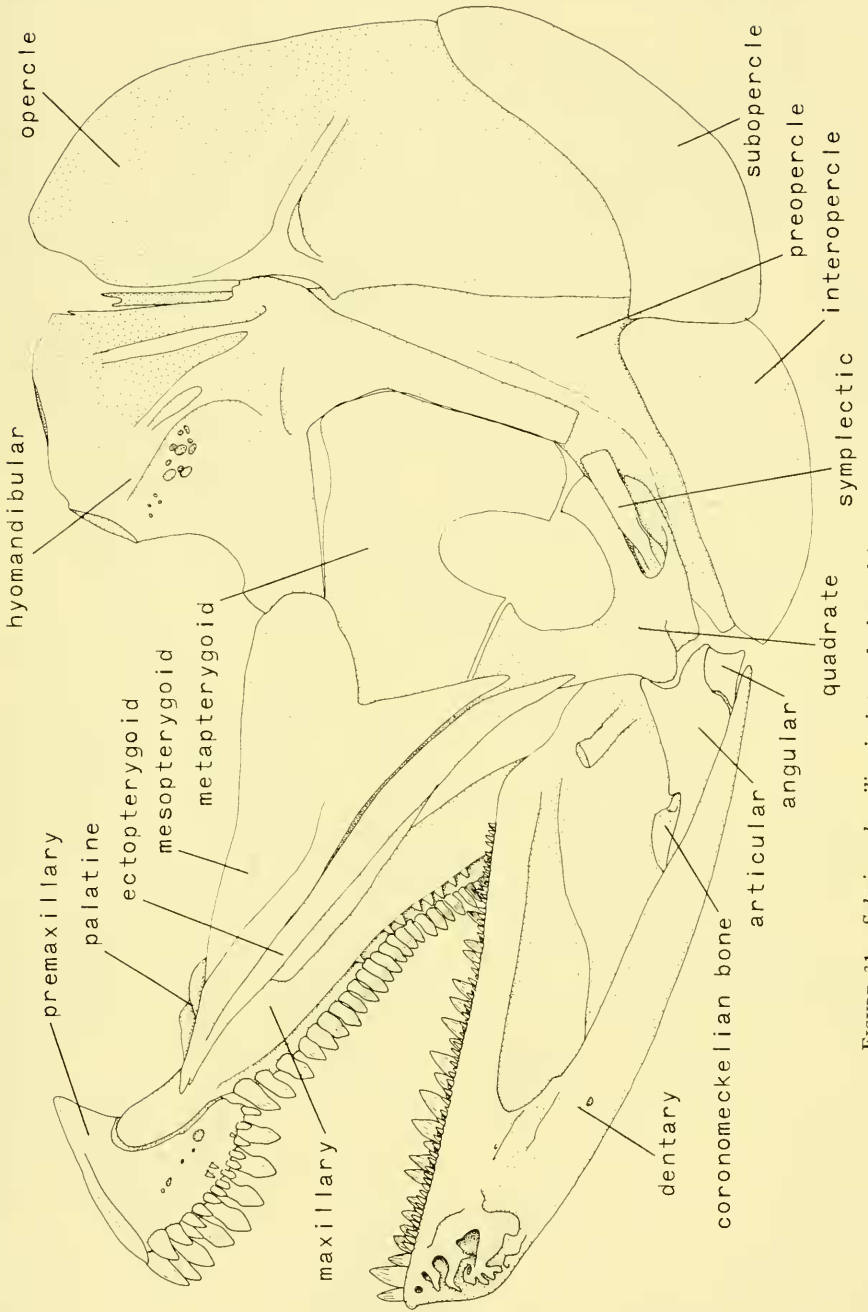


FIGURE 31. *Salminus brasiliensis*, internal view of jaws and deeper facial bones.

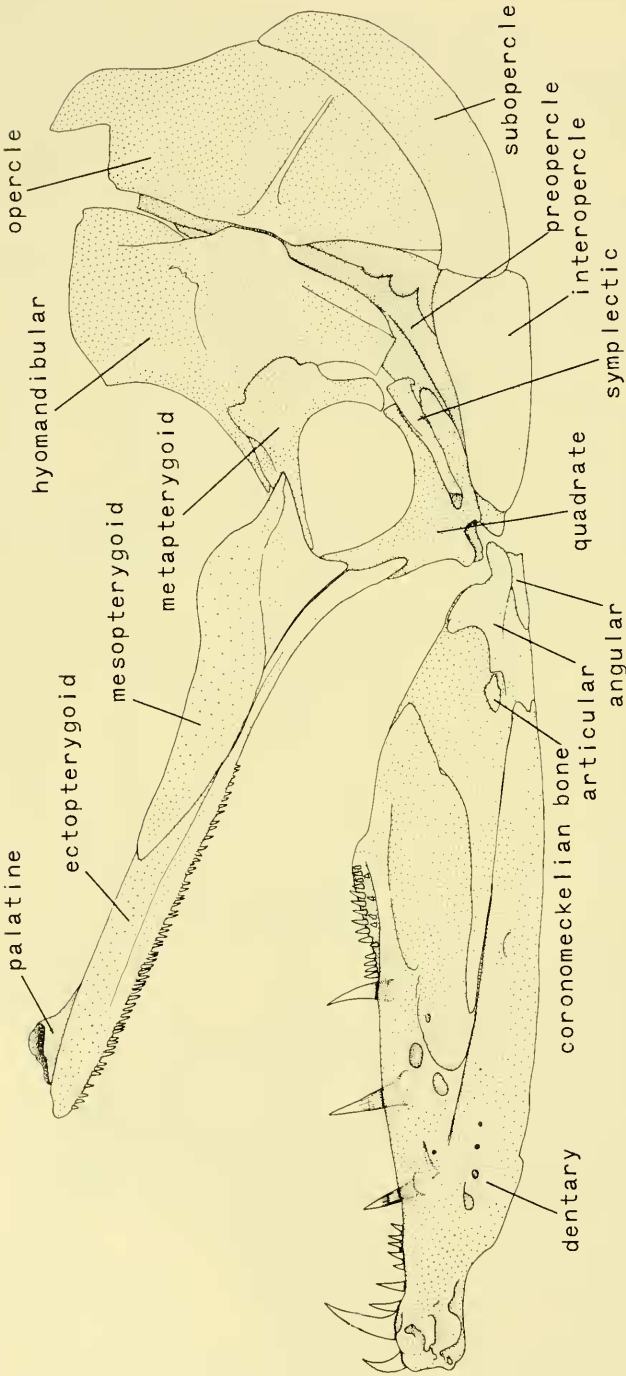


FIGURE 32. *Acetrorhynchus* species, internal view of lower jaw, palatal bones and deeper facial bones.

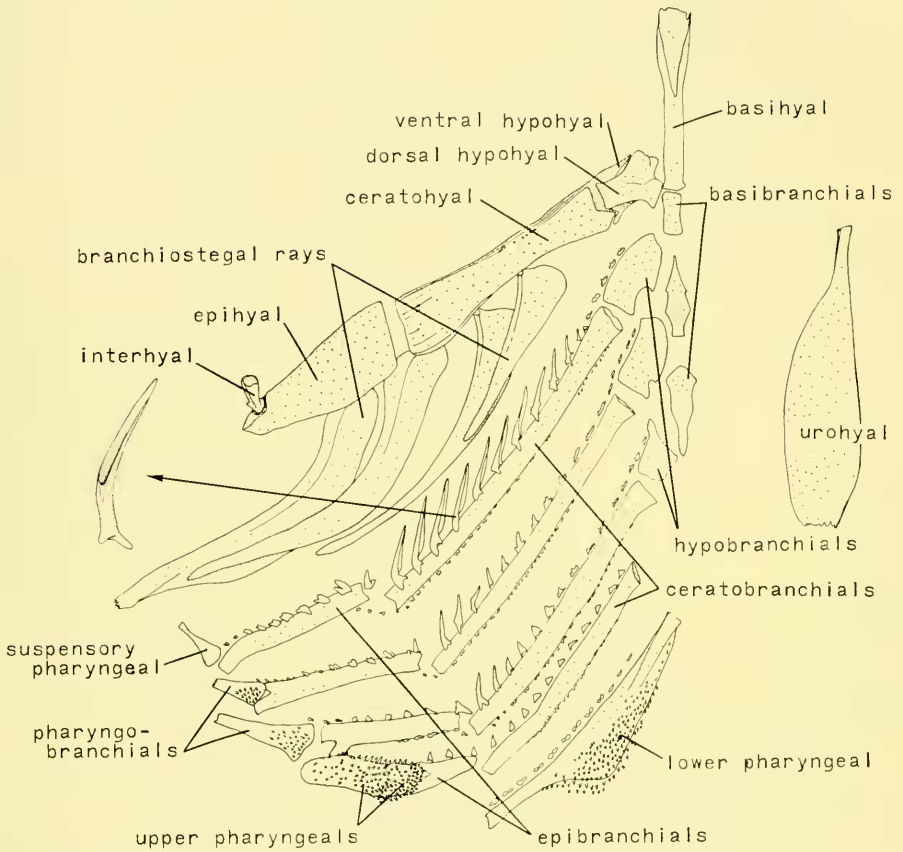


FIGURE 33. *Hepsetus odoe*, dorsal view of hyobranchial arches. The dorsalmost branchial elements have been pinned out to the side.

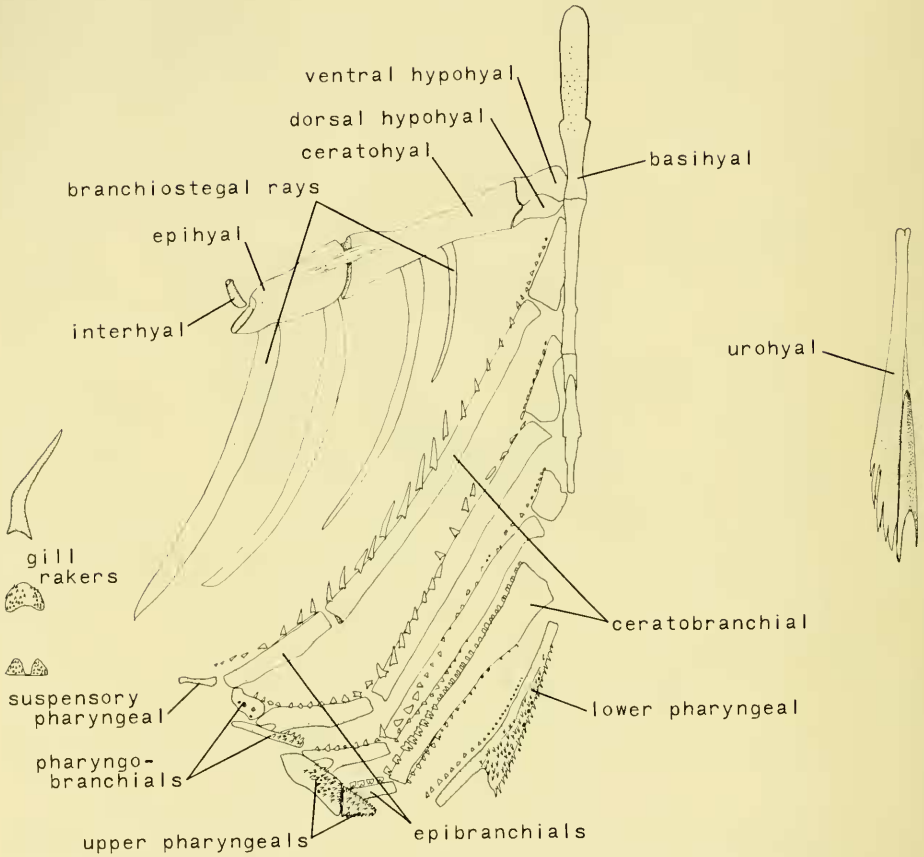


FIGURE 34. *Ctenolucius hujeta*. Dorsal view of hyobranchial arches. The dorsalmost branchial elements have been pinned out to the side.

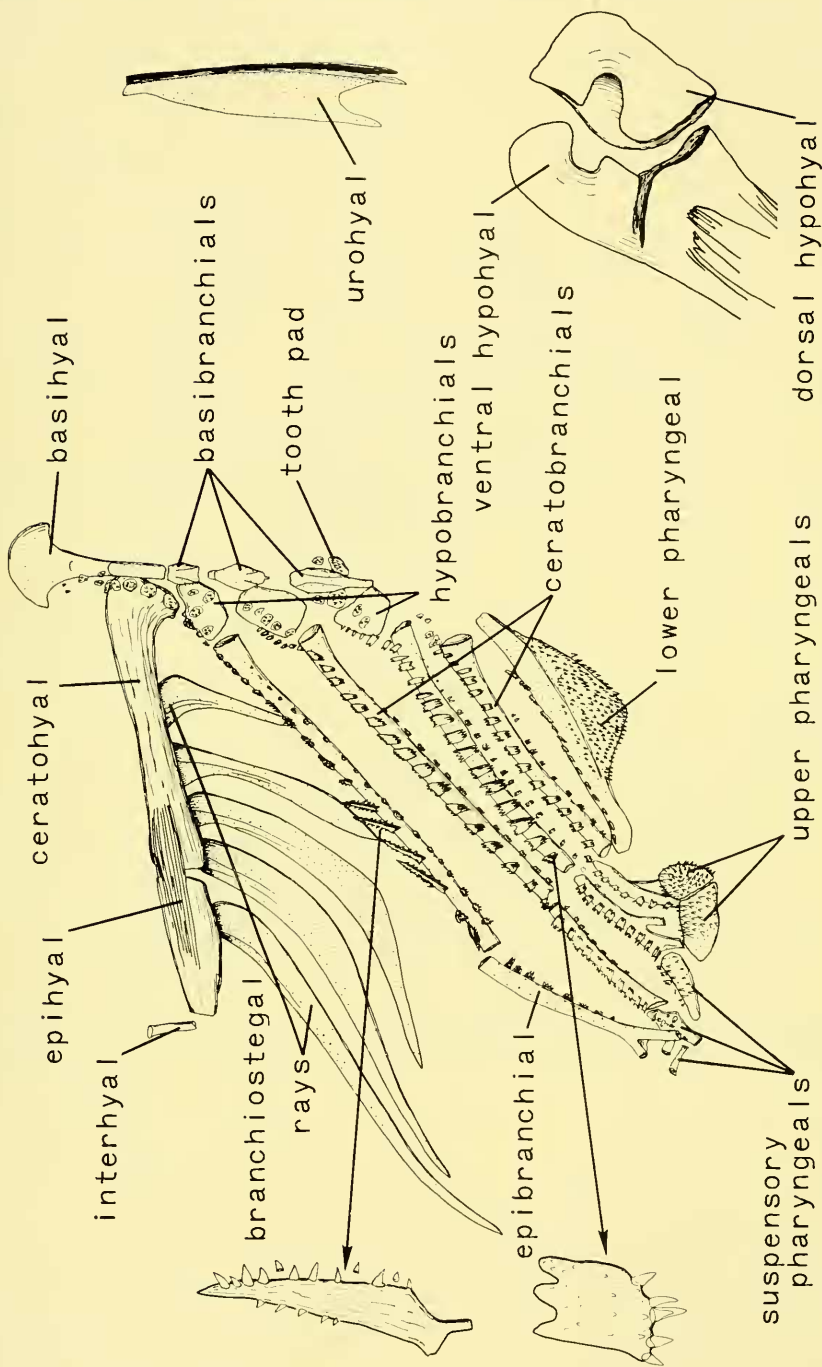


FIGURE 35. *Hoplias* species, dorsal view of hyobranchial arches. The dorsalmost branchial elements have been pinned out to the side.

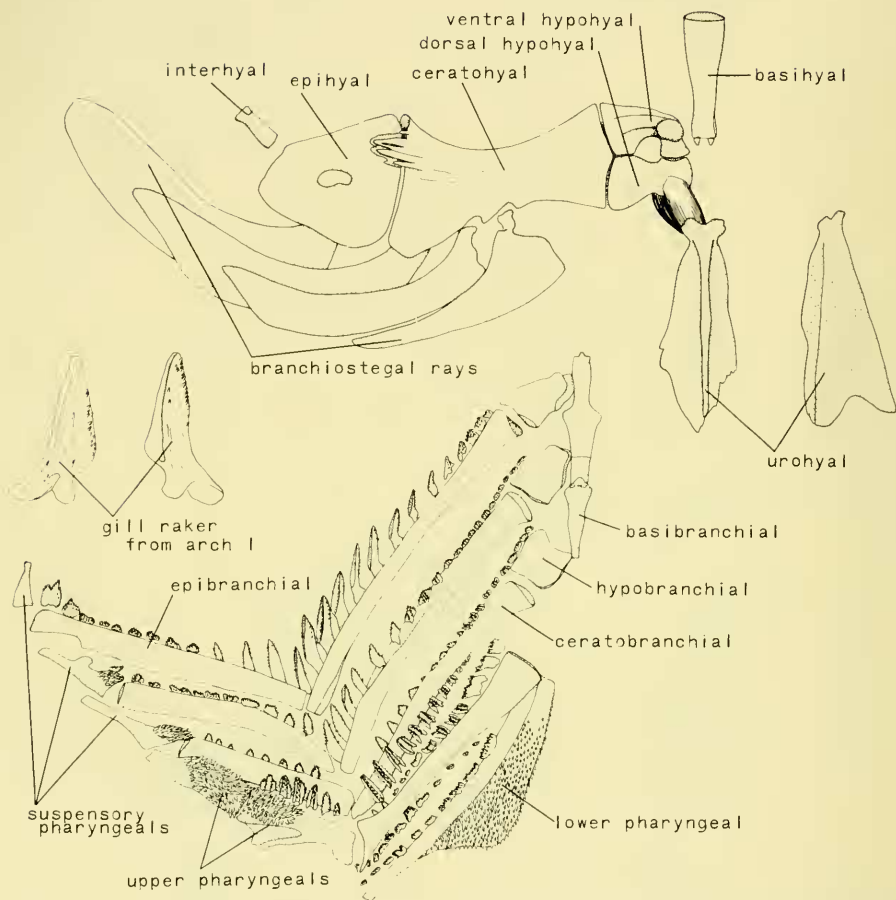


FIGURE 36. *Salminus brasiliensis*, dorsal view of hyobranchial arches. The dorsalmost branchial elements have been pinned out to the side.

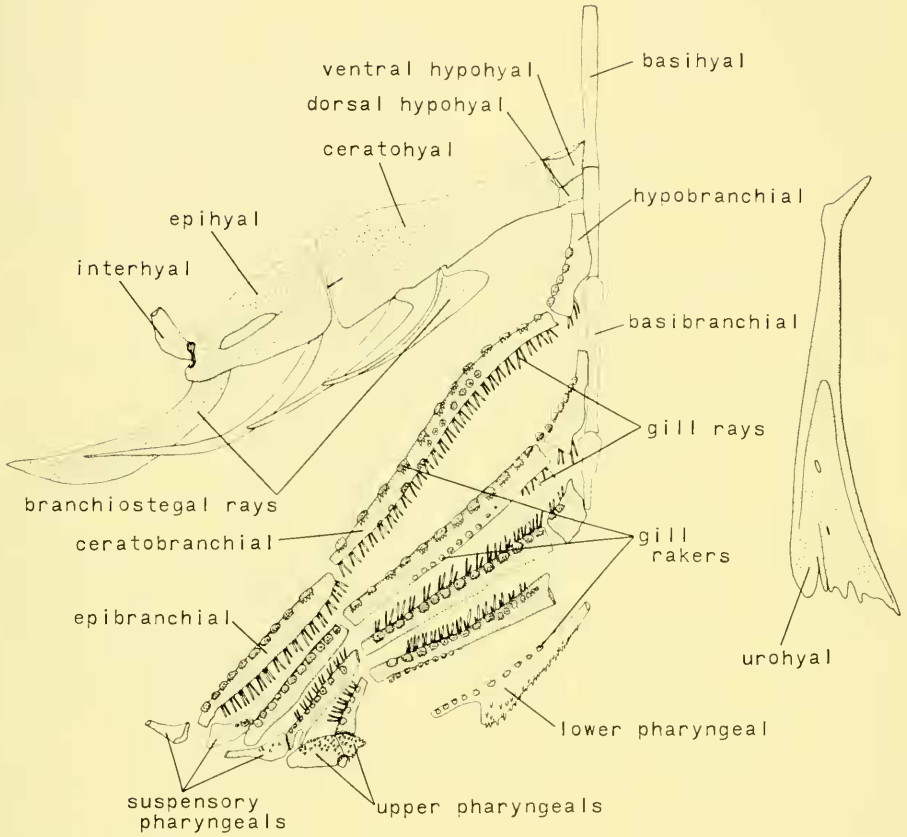


FIGURE 37. *Acetrorhynchus* species, dorsal view of hyobranchial arches. The dorsalmost branchial elements have been pinned out to the side.

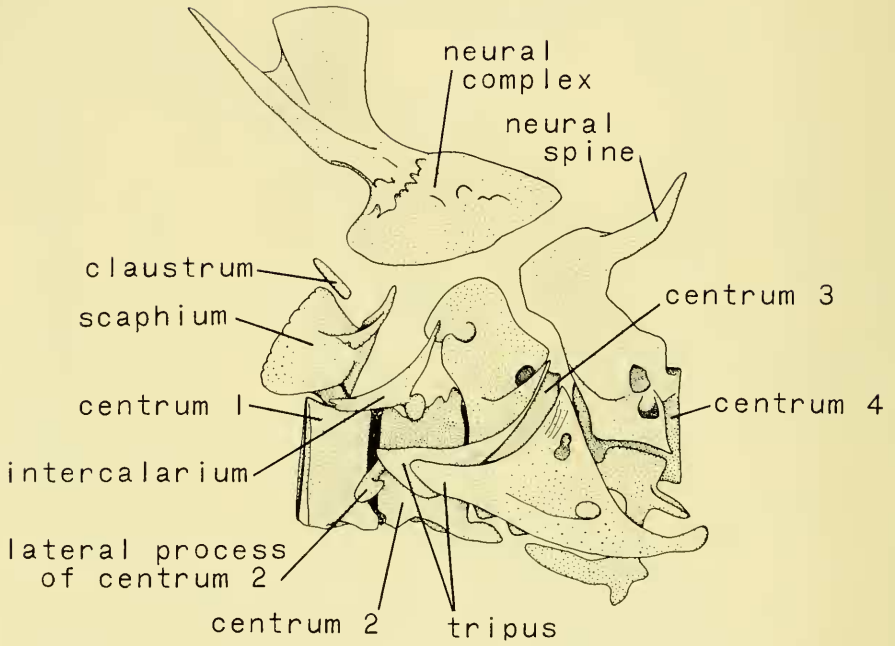


FIGURE 38. *Hepsetus odoe*, lateral view of Weberian apparatus.

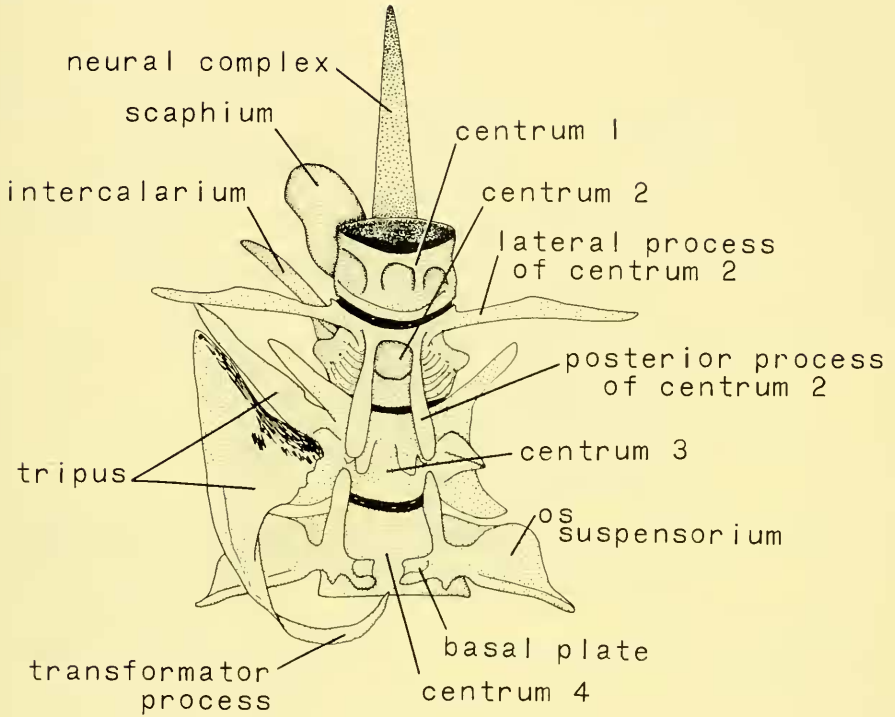


FIGURE 39. *Hepsetus odoe*, ventral view of Weberian apparatus.

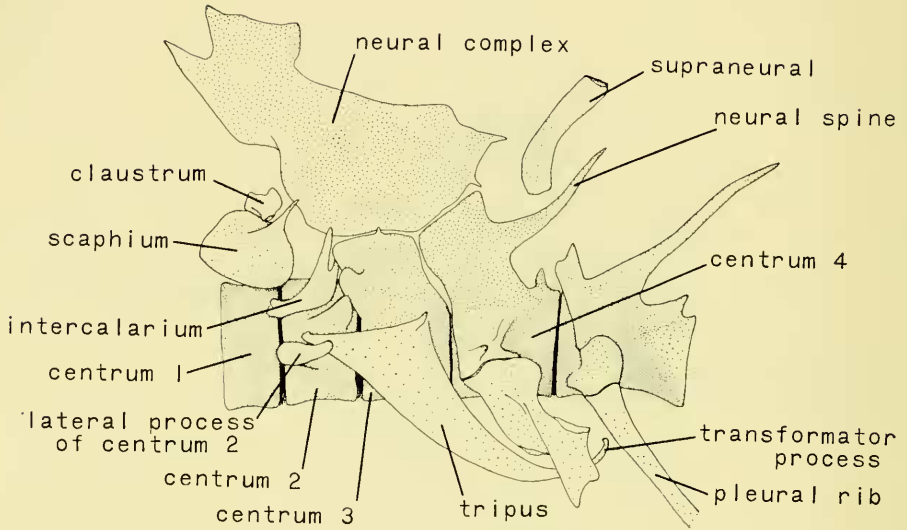


FIGURE 40. *Ctenolucius hujeta*, lateral view of Weberian apparatus and fifth vertebra.

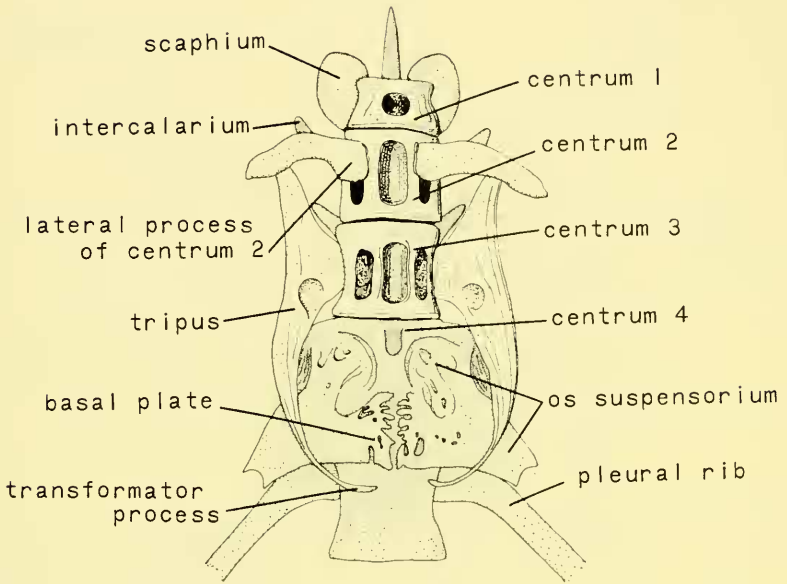


FIGURE 41. *Ctenolucius hujeta*, ventral view of Weberian apparatus and fifth vertebra.

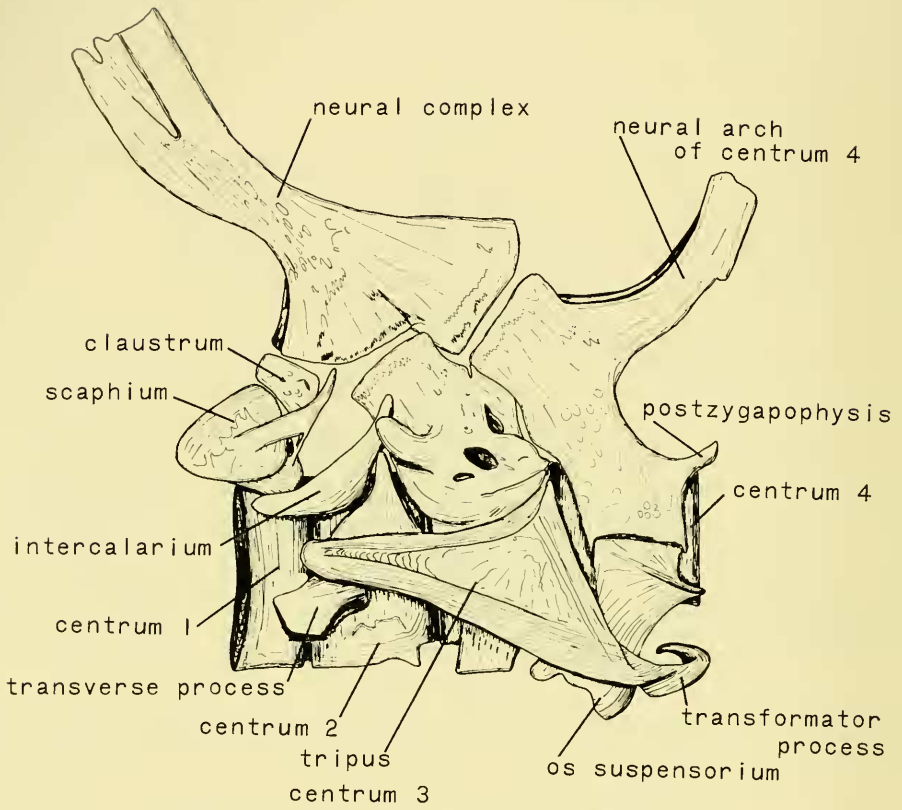


FIGURE 42. *Hoplias* species, lateral view of Weberian apparatus.

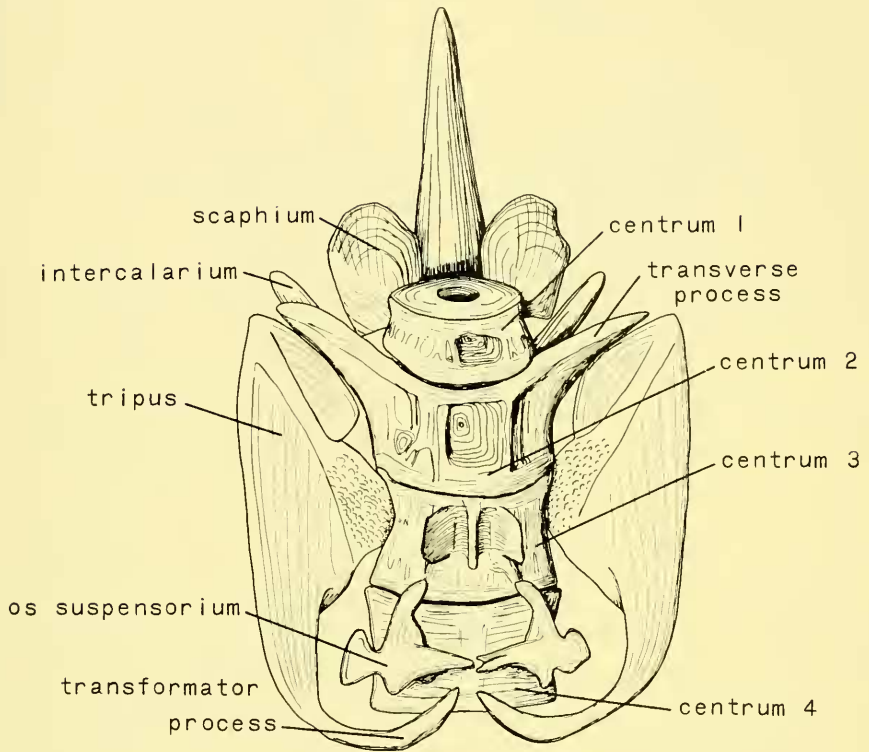


FIGURE 43. *Hoplias* species, ventral view of Weberian apparatus.

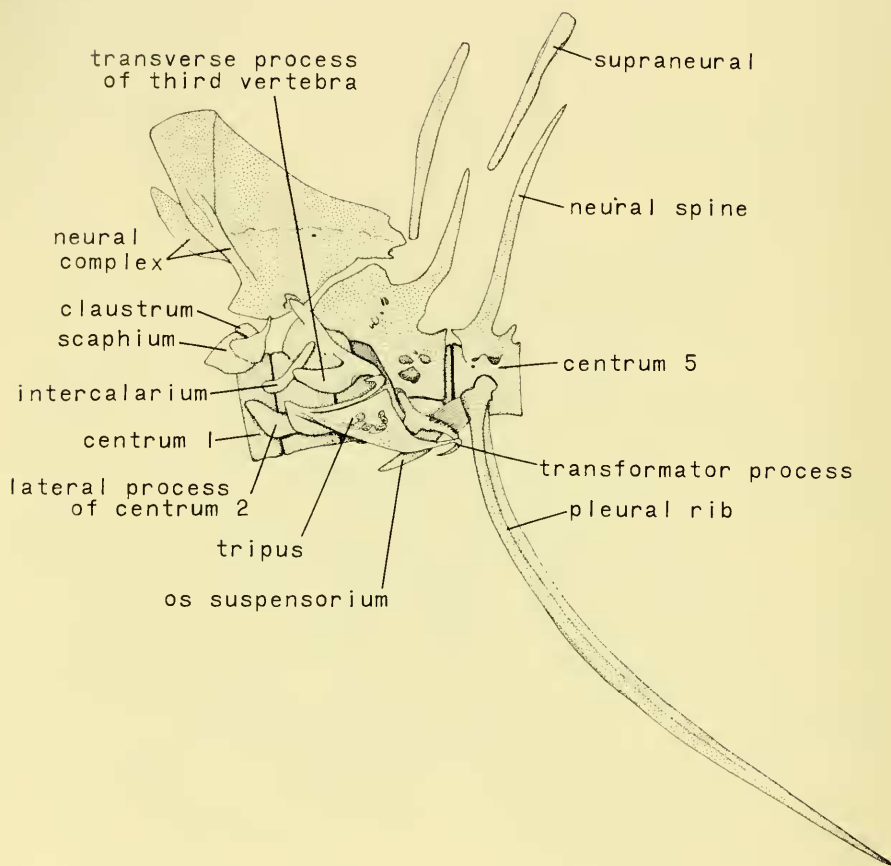


FIGURE 44. *Salminus brasiliensis*, lateral view of Weberian apparatus and fifth vertebra.

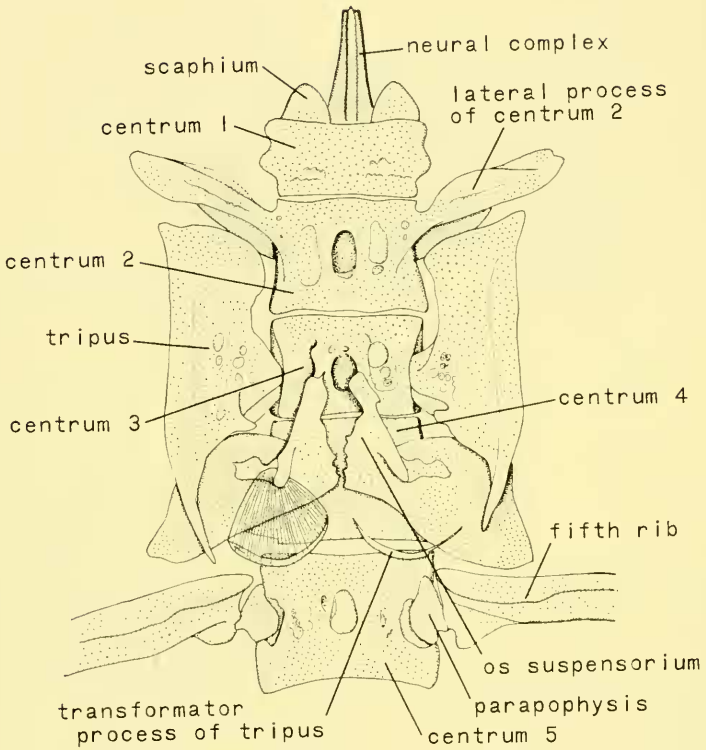


FIGURE 45. *Salminus brasiliensis*, ventral view of Weberian apparatus and fifth vertebra.

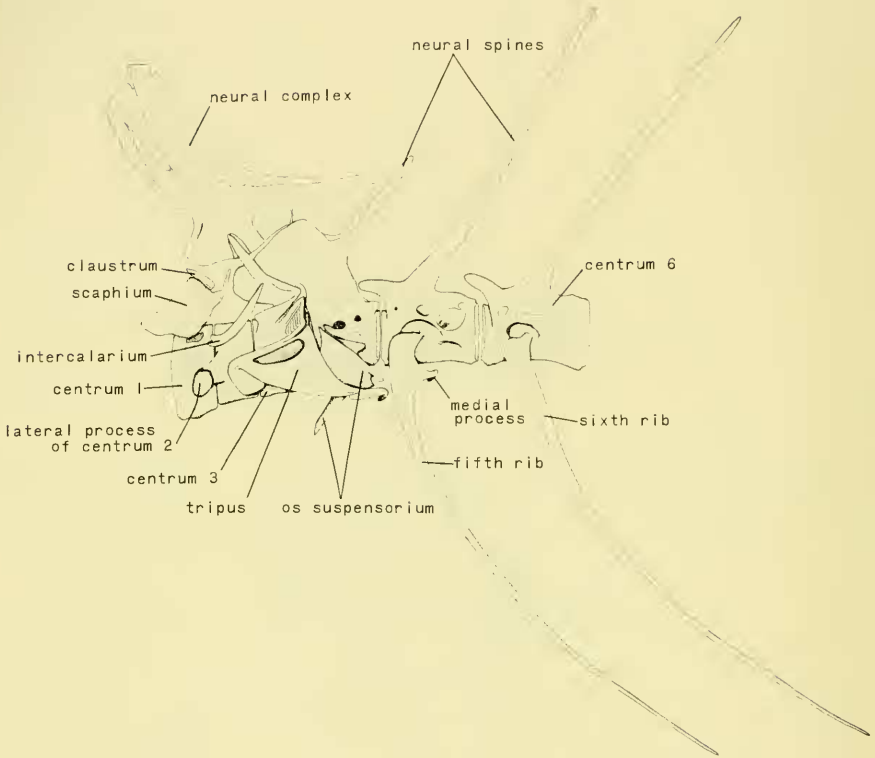


FIGURE 46. *Acestorhynchus* species, lateral view of Weberian apparatus and fifth and sixth vertebrae.

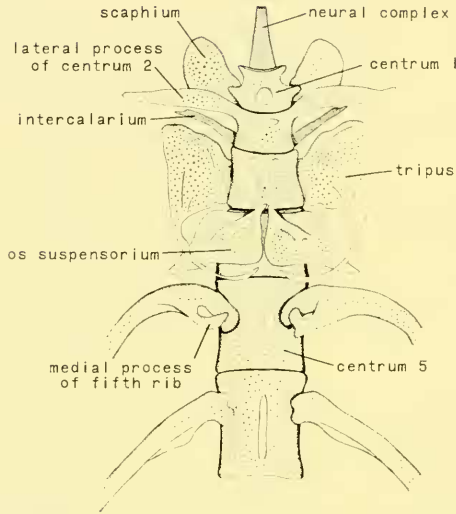


FIGURE 47. *Acestrorhynchus* species, ventral view of Weberian apparatus and fifth and sixth vertebrae.

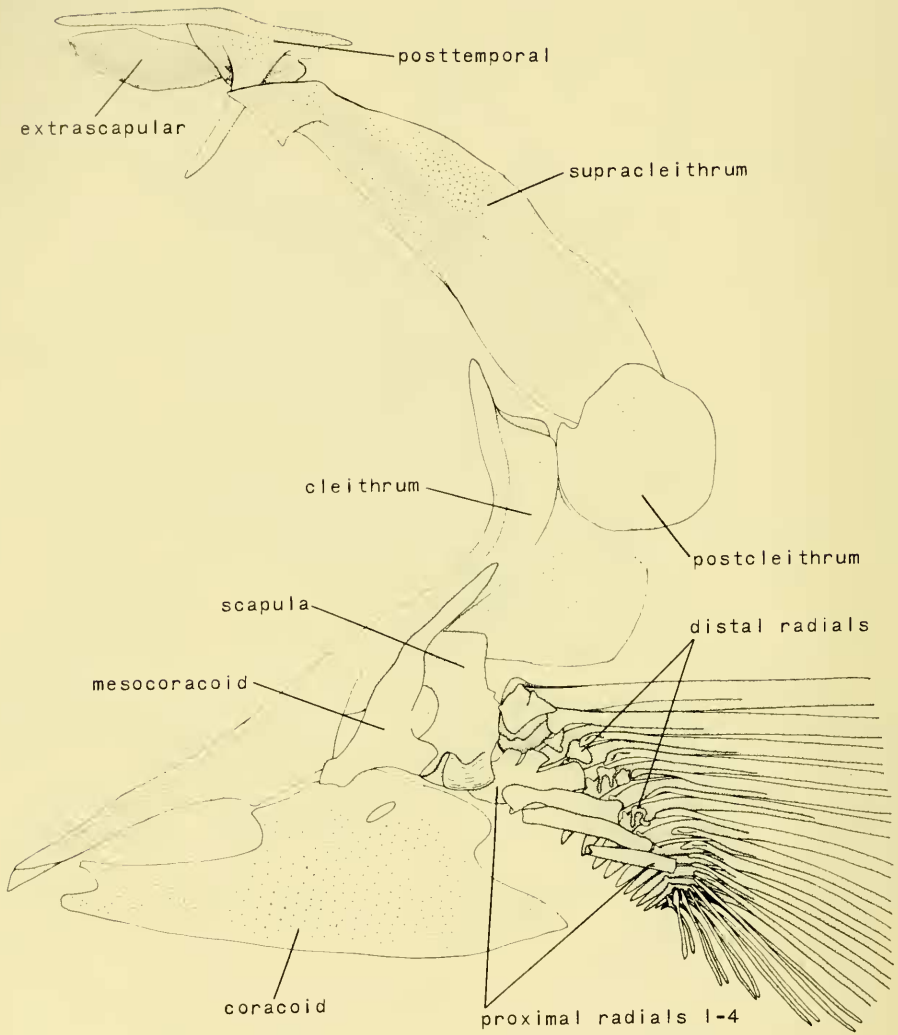


FIGURE 48. *Hepsetus odoe*, internal view of right pectoral girdle.

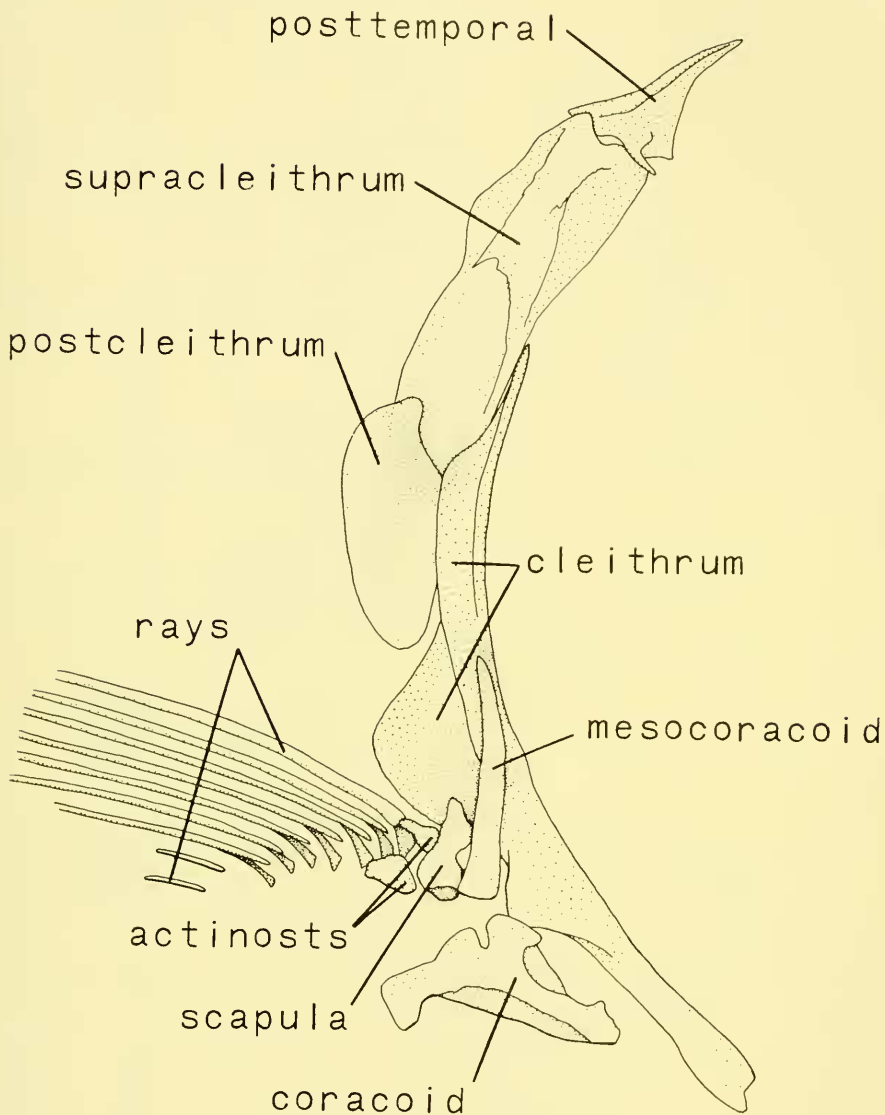


FIGURE 49. *Hepsetus odoc*, internal view of left pectoral girdle of a 42 mm. specimen.

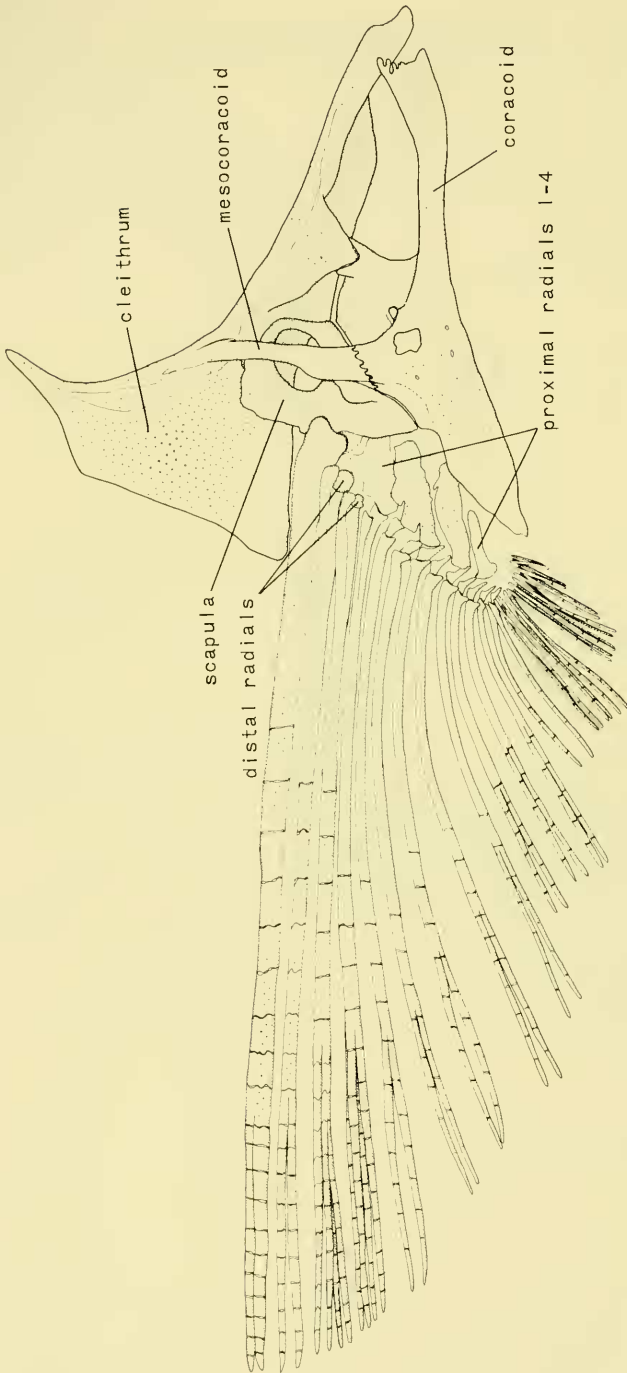


FIGURE 50. *Ctenolucius hujeta*, internal view of the primary pectoral girdle of the left side (the secondary girdle is shown attached to the cranium in fig. 12).

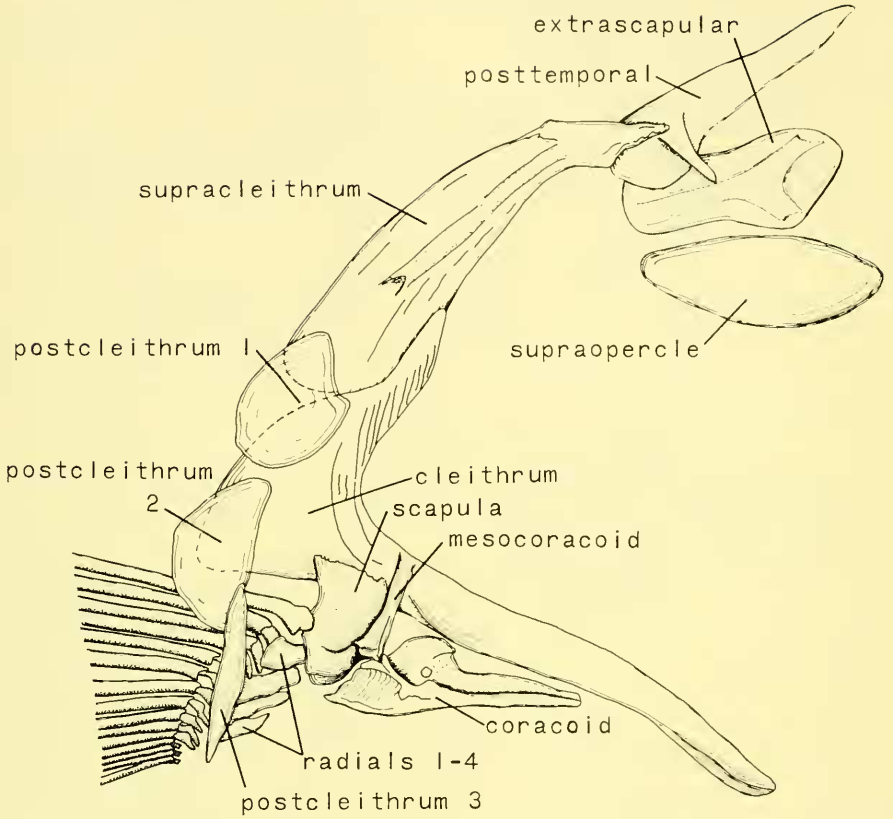


FIGURE 51. *Hoplias* species, internal view of left pectoral girdle.

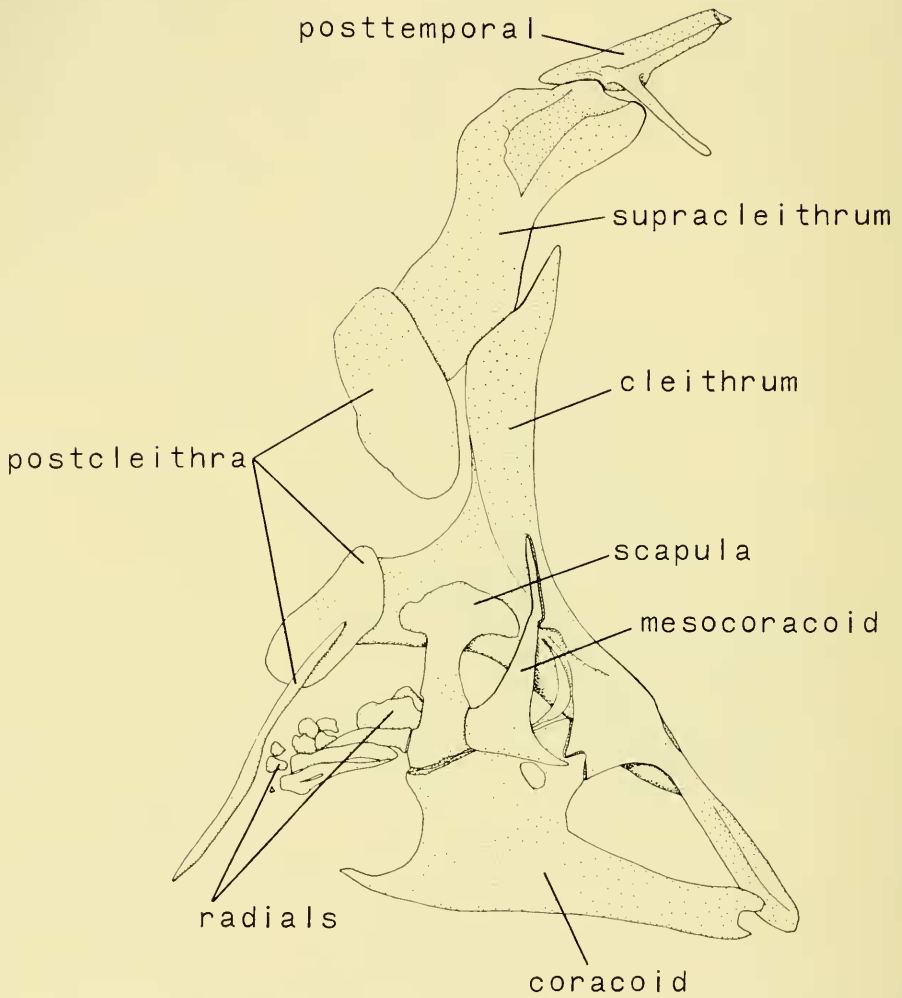


FIGURE 52. *Acestorhynchus* species, internal view of left pectoral girdle.

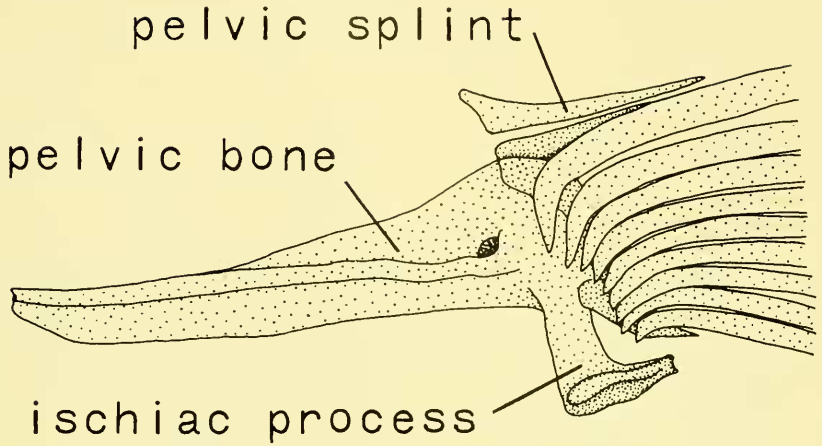


FIGURE 53. *Hepsetus odoe*, ventral view of pelvic girdle.

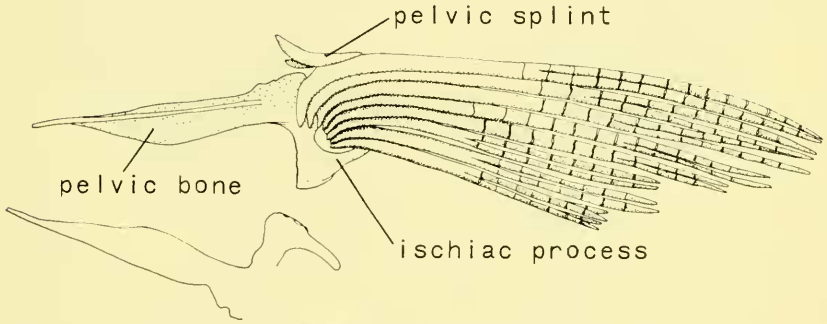


FIGURE 54. *Ctenolucius hujeta*, ventral view of pelvic girdle.

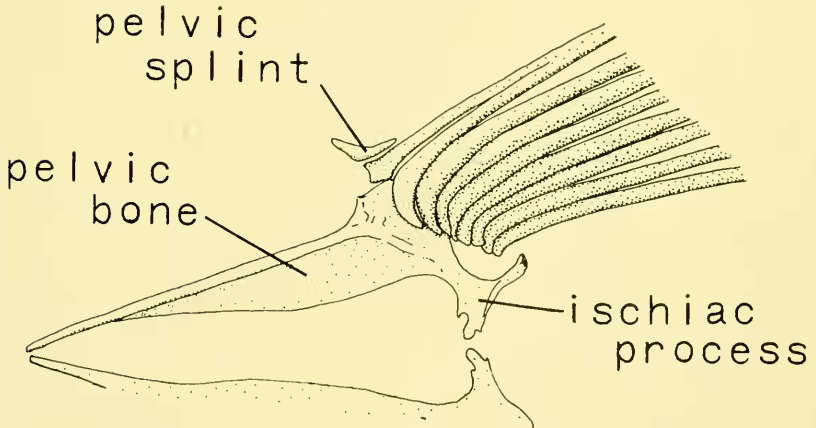


FIGURE 55. *Hoplias* species, ventral view of pelvic girdle.

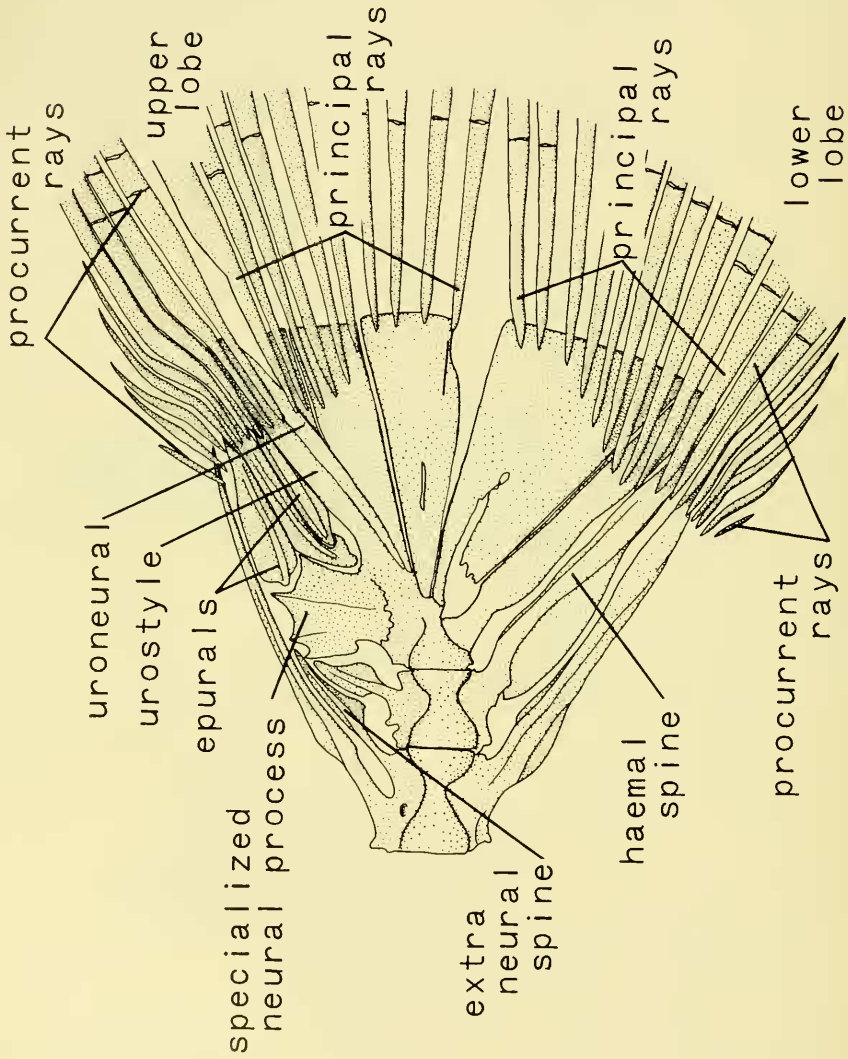


FIGURE 56. *Hepsetus odoe*, lateral view of caudal skeleton.

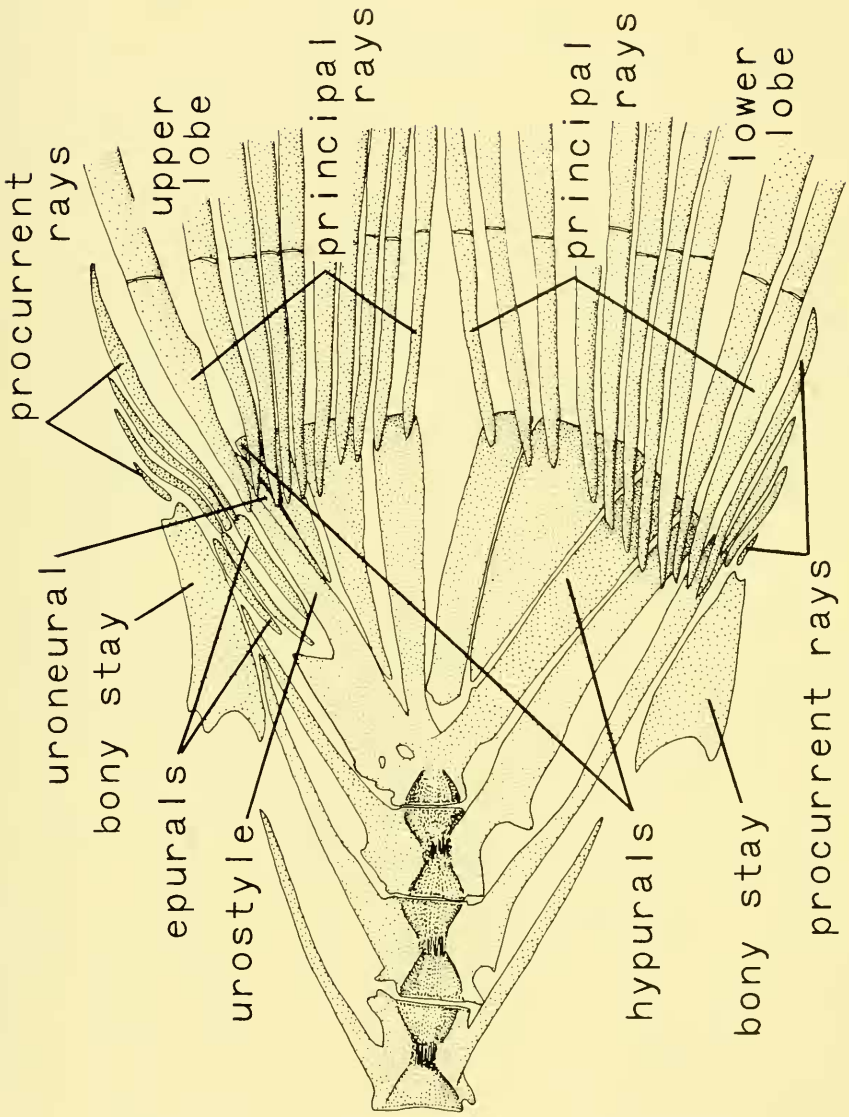


FIGURE 57. *Ctenolucius hujeta*, lateral view of caudal skeleton.

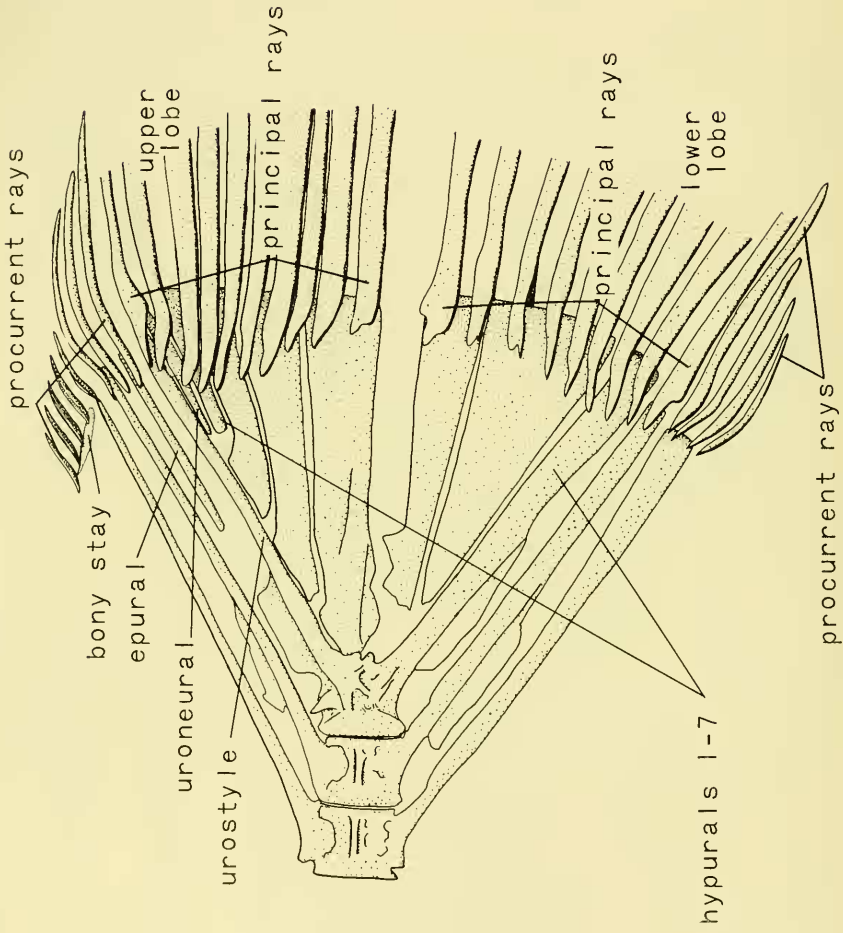


FIGURE 58. *Hoplias* species, lateral view of caudal skeleton.

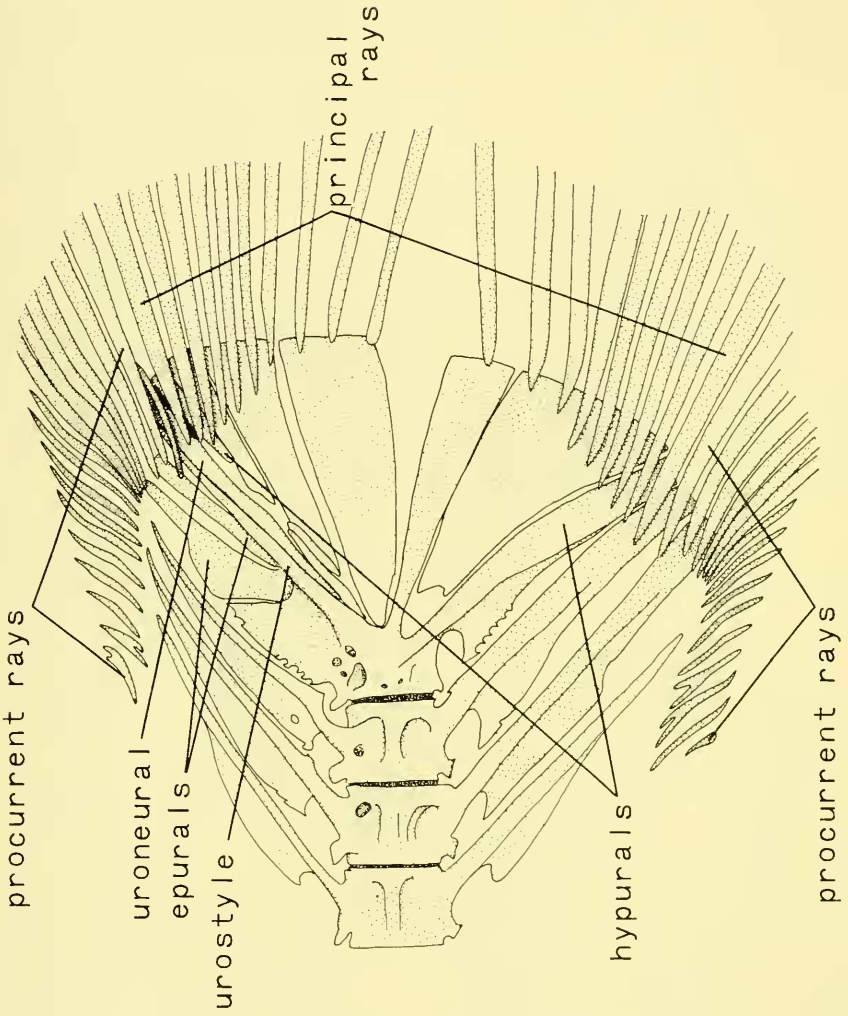


FIGURE 59. *Sabminus brasiliensis*, lateral view of caudal skeleton.

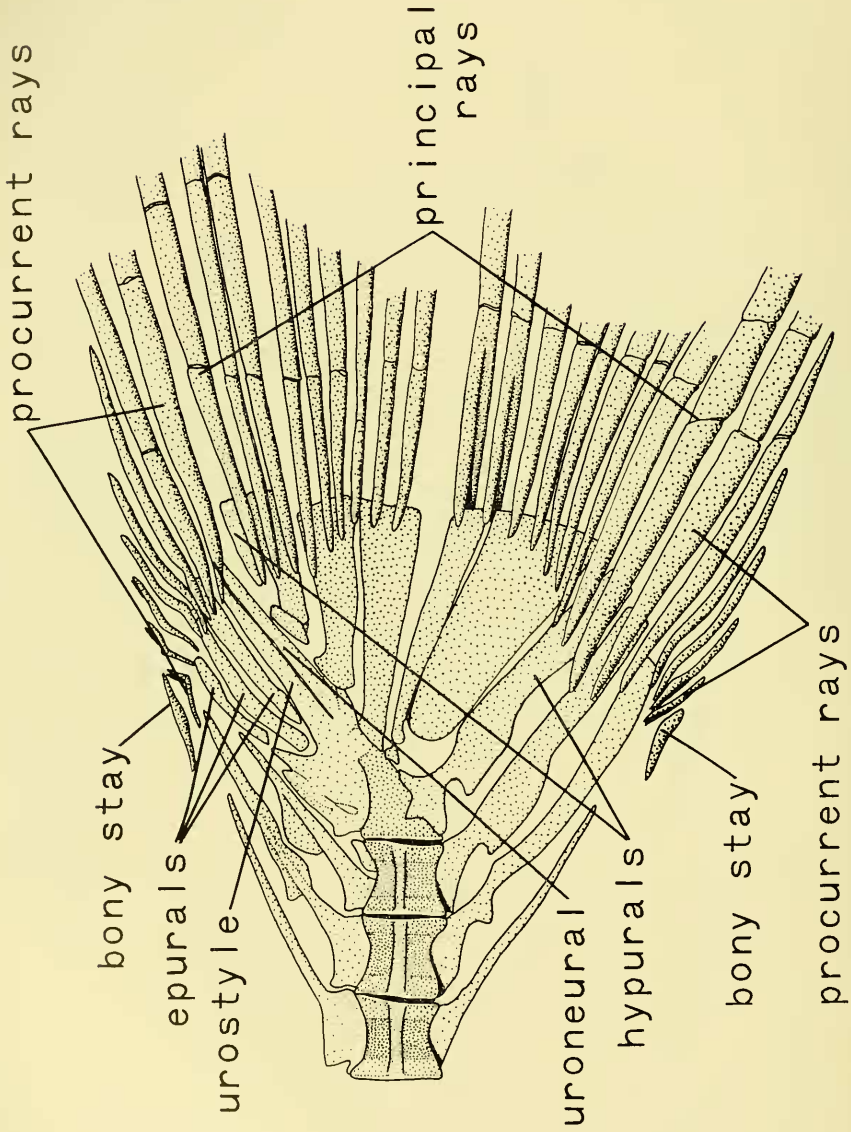


FIGURE 60. *Hydrocynus* species, lateral view of caudal skeleton of a 20 mm. specimen.

LITERATURE CITED

- ADAMS, LEVERETT A.
1940. Some characteristic otoliths of American Ostariophysi. *Journal of Morphology*, vol. 66, no. 3, pp. 497-527, 4 pls.
- ALEXANDER, R. MCN.
1965. Adaptation in the skulls and cranial muscles of South American characinoid fish. *Journal of the Linnaean Society. Zoology*, vol. 45, no. 305, pp. 169-190.
- ALLIS, EDWARD P.
1897. The cranial muscles and cranial and first spinal nerves in *Amia calva*. *Journal of Morphology*, vol. 12, no. 3, pp. 487-814, pls. 20-39.
- BERRY, FREDERICK H.
1964. Aspects of the development of the upper jaw bones in teleosts. *Copeia*, 1964, no. 1, pp. 375-384.
- BERTMAR, GUNNAR
1959. On the ontogeny of the chondral skull in Characidae, with a discussion of the chondrocranial base and the visceral chondrocranium in fishes. *Acta Zoologica*, vol. 40, nos. 2-3, pp. 203-364.
- BÖHLKE, JAMES
1953. A minute new herring-like characid fish genus adapted for plankton feeding, from the Rio Negro. *Stanford Ichthyological Bulletin*, vol. 5, no. 1, pp. 168-170.
1958. Studies on fishes of the family Characidae. No. 14. A report on several extensive recent collections from Ecuador. *Proceedings of the Academy of Natural Sciences of Philadelphia*, vol. 110, pp. 1-121, 7 pls.
- BOULENGER, GEORGE A.
1909. Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History). London, vol. 1, pp. xi + 373.
- EASTMAN, CHARLES R.
1917. Dentition of *Hydrocyon* and its supposed fossil allies. *Bulletin of the American Museum of Natural History*, vol. 37, art. 24, pp. 757-760, pls. 84-87.
- EIGENMANN, CARL H.
1915. The Cheirodontinae, a subfamily of minute characid fishes of South America. *Memoirs of the Carnegie Museum*, vol. 12, no. 1, 99 pp., 77 pls.
- EIGENMANN, CARL H., AND A. A. NORRIS
1900. Sobre alguns peixes de S. Paulo, Brazil. *Revista do Museu Paulista*, vol. IV, pp. 349-362.
- FUSTER DE PLAZA, MARIA L.
1950. Una contribución al conocimiento del dorado *Salminus maxillosus* Cuv. y Val. *Revista del Museo de La Plata*, n. s., vol. 6, zool., no. 4, pp. 171-214, 2 pls.
- GÉRY, JACQUES
1963a. Essai sur les affinités phylogénétiques des *Agoniates* et l'origine des Characidae, à propos de la description d'une forme nouvelle de l'Amazone péruvienne: *Agoniates ladigesii*. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, vol. 60, pp. 265-284.
1963b. Paired frontal foramina in living teleosts: definition of a new family of characid fishes, the Crenuchidae. *Nature*, vol. 198, no. 4879, pp. 502-503.
1963c. L'appareil protracteur buccal de *Bivibranchia* (Characoidei) (I) avec une note sur *Phractolaemus* (Chanoidei) (Pisces). *Vie et Milieu*, vol. 13, no. 4, pp. 729-740.

1964. A review of the Chilodinae, with a key to the species. *Tropical Fish Hobbyist*, May, 1964, pp. 5-10, 63-67.
1966. Endemic characoid fishes from the upper Rio Cauca at Cali, Colombia. *Ichthyologica, the Aquarium Journal*, vol. 37, no. 1, pp. 13-24.
- GÉRY, JACQUES, AND VU-TÂN-TUÊ
1963. Définitions de *Cynopotamus* Val. et genres voisins (Pisces, Characoidei). *Bulletin du Muséum National d'Histoire Naturelle*, 2nd ser., vol. 35, nos. 2 and 3, pp. 143-150 and 238-246.
- GILL, THEODORE N.
1861. Catalogue of the fishes of the eastern coast of North America, from Greenland to Georgia. *Proceedings of the Academy of Natural Sciences of Philadelphia*, vol. 13, supplement, pp. 1-63.
- 1895a. Notes on characinoid fishes with ctenoid scales, with a description of a new *Psectrogaster*. *Proceedings of the United States National Museum*, vol. 18, no. 1055, pp. 199-203.
- 1895b. The differential characters of characinoid and erythrinoid fishes. *Proceedings of the United States National Museum*, vol. 18, no. 1056, pp. 205-209.
- GOSLINE, WILLIAM A.
1951. Notes on the characid fishes of the subfamily Serrasalminae. *Proceedings of the California Academy of Sciences*, vol. 27, no. 2, pp. 17-64.
1961. Some osteological features of modern lower teleostean fishes. *Smithsonian Miscellaneous Collections*, vol. 142, no. 3, pp. 1-42.
1965. Teleostean phylogeny. *Copeia*, 1965, no. 2, pp. 186-194.
- GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS
1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History*, vol. 131, art. 4, pp. 339-455.
- GREGORY, WILLIAM K., AND G. M. CONRAD
1937. The structure and development of the complex symphyseal hinge joint in the mandible of *Hydrocynus lineatus* Bleeker, a characin fish. *Proceedings of the Zoological Society of London*, 1936, pp. 957-984.
1938. The phylogeny of the characin fishes. *Zoologica (New York)*, vol. 23, pp. 319-360.
- HUBBS, CARL L.
1919. A comparative study of the bones forming the opercular series of fishes. *Journal of Morphology*, vol. 33, no. 1, pp. 61-71.
1939. *Hepsetus* to replace *Hydrocynoides* and *Sarcodaces* for a genus of African freshwater fishes. *Copeia*, 1939, no. 3, p. 168.
- MONOD, THEODORE
1950. Notes d'ichtyologie ouest-africaine. *Bulletin de l'Institut Français d'Afrique Noire*, vol. 12, no. 1, pp. 1-71.
- MÜLLER, JOHANNES, AND F. H. TROSCHEL
1845. *Horae ichthyologiae. Beschreibung und Abbildung neuer Fische. I, II. Die Familie der Characinen.* Berlin, pp. 1-40, 11 pls.
- MYERS, GEORGE S.
1958. Trends in the evolution of teleostean fishes. *Stanford Ichthyological Bulletin*, vol. 7, no. 3, pp. 27-30.
1966. Derivation of the freshwater fish fauna of Central America. *Copeia*, 1966, no. 4, pp. 766-773.

NELSON, EDWARD M.

1949. The swim bladder and Weberian apparatus of *Rhaphiodon vulpinus* Agassiz, with notes on some additional morphological features. *Journal of Morphology*, vol. 84, pp. 495-523, 6 pls.

NORRIS, KENNETH S., AND J. H. PRESCOTT

1959. Jaw structure and tooth replacement in the opaleye, *Girella nigricans* (Ayres) with notes on other species. *Copeia*, 1959, no. 4, pp. 275-283, 1 table.

POLL, MAX

1957. Les genres des poissons d'eau douce de l'Afrique. *Annales du Musée Royale de l'Afrique Centrale*, octavo ser., zool., no. 54, 191 pp.

REGAN, CHARLES TATE

1911. The classification of the teleostean fishes of the order Ostariophysi.—I. Cyprinoidae. *Annals and Magazine of Natural History*, ser. 8, vol. 8, pp. 13-32, pl. 2.

RIDWOOD, WALTER G.

1904. On the cranial osteology of the fishes of the families Elopidae and Albulidae, with remarks on the morphology of the skull in the lower teleostean fishes generally. *Proceedings of the Zoological Society of London*, vol. 2 [1904], pp. 35-81.

ROBERTS, TYSON R.

1966. Description and osteology of *Lepidarchus adonis*, a remarkable new characid fish from West Africa. *Stanford Ichthyological Bulletin*, vol. 8, no. 3, pp. 209-227.
- 1967a. Tooth formation and replacement in characid fishes. *Stanford Ichthyological Bulletin*, vol. 8, no. 4, pp. 231-247.
- 1967b. *Virilia*, a new genus of sexually dimorphic characid fishes from West Africa, with remarks on characoids having an incomplete lateral line. *Stanford Ichthyological Bulletin*, vol. 8, no. 4, pp. 251-259.

ROWNTREE, WALTER S.

1903. On some points in the visceral anatomy of the Characinidae, with an enquiry into the relations of the ductus pneumaticus in the Physostomi generally. *Transactions of the Linnaean Society of London*, 2nd ser., vol. 9, pp. 47-81, pls. 3-4.
1906. On the dentition of the characinoid genus *Piabuca*: a new generic character. *Annals and Magazine of Natural History*, 7th ser., vol. 17, no. 98, pp. 240-243.

SAGEMEHL, M.

1885. Beiträge zur vergleichenden Anatomie der Fische, III. Das Cranium der Characiniden nebst allgemein Bemerkungen über die mit einem Weber'schen Apparat versehenen Physostomen-familien. *Morphologische Jahrbücher*, vol. 10, pp. 1-119, pls. 1-2.

STARKS, EDWIN C.

1926. Bones of the ethmoid region of the fish skull. *Stanford University Publications, University Series, Biological Sciences*, vol. 4, no. 3, pp. 137-338.
1930. The primary shoulder girdle of the bony fishes. *Stanford University Publications, University Series, Biological Sciences*, vol. 6, no. 2, pp. 1-93 (also numbered 147-239).

STEINDACHNER, FRANZ

1878. Zur Fisch-Fauna des Magdalenen-Stromes. *Denkschriften der Kaiserlichen Akademie der Wissenschaften*, vol. 39, no. 1, pp. 19-78, 15 pls.
1880. Zur Fisch-Fauna des Cauca und der Flüsse bei Guayaquil. *Denkschriften der Kaiserlichen Akademie der Wissenschaften*, vol. 42, no. 1, pp. 55-104, 9 pls.

TCHERNAVIN, V. V.

1953. The feeding mechanisms of the deep sea fish *Chauliodus sloani* Schneider. *London (British Museum, Nat. Hist.)*, viii + 101 pp., 10 pls.

THYS VAN DEN AUDENAERDE, D. F. E.

1961. L'anatomie de *Phractolaemus ansorgei* Blgr. et la position systématique des Phractolaemidae. Annales du Musée Royale de l'Afrique Centrale, Tervuren, ser. octavo, zool. sci., no. 103, pp. 101-167.

WEITZMAN, STANLEY H.

1954. The osteology and relationships of the South American characid fishes of the subfamily Gasteropelecinae. Stanford Ichthyological Bulletin, vol. 4, no. 4, pp. 212-263.
- 1960a. Further notes on characid fossils. Stanford Ichthyological Bulletin, vol. 7, no. 4, pp. 215-216.
- 1960b. Further notes on the relationships and classification of the South American fishes of the subfamily Gasteropelecinae. Stanford Ichthyological Bulletin, vol. 7, no. 4, pp. 217-239.
1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. Stanford Ichthyological Bulletin, vol. 8, no. 1, pp. 1-77.
1964. Osteology and relationships of South American characid fishes of subfamilies Lebiasinae and Erythrinae with special reference to subtribe Nannostomina. Proceedings of the United States National Museum, vol. 116, no. 3499, pp. 127-169.
1967. The origin of the stomiatoïd fishes with comments on the classification of salmoniform fishes. Copeia, 1967, no. 3, pp. 507-540.